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Macroevolutionary Diversification of Multivariate Body Plan in a Prominent Lizard Adaptive Radiation

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Contents

List of Tables and Figures

Tables

Figures

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1 Abstract

Natural selection theory predicts that similar ecological pressures can result in similar phenotypes evolving in distantly related species through a process known as convergent evolution. Although there are many described cases of species adaptively evolving similar phenotypes in response to the same habitats (i.e., "ecomorphs"), this is not a universal outcome of natural selection. *Liolaemus* lizards embody an exceptional example of adaptive radiation where, thus far, studies have not identified any evidence of ecomorphological evolution. Why some lineages display such signals of convergent evolution while others do not remains an open question. Here, shape was more accurately quantified by using geometric morphometrics (as opposed to the linear measures of morphology used previously) to address the question of whether *Liolaemus* lizards have undergone convergent evolution in body morphology and to conduct phylogenetic modelling to quantify patterns and rates of multivariate morphological evolution in this radiation. Further to this, the effect of diet and parity mode on morphology were explored. The morphometric analysis produced three principal component (PC) axes that explained over 10% of variance. Each axis captures different changes in shape; PC1 shows a reduction in relative head size when the body becomes wider and more elongated and vice versa. PC2 shows changes in the width of the body, with little change in the length of the body and of changes in the head. PC3 shows lengthening in the posterior of the body while there is a pinching towards the front of the body and an increase in relative head size and vice versa. Results generally showed no significant separation in body shape between microhabitat groups, and thus suggest ecomorphs are not present. Diet and parity groups were significantly separated, however, not when phylogeny was included in the analyses. Phylogenetic macroevolutionary analyses were used to develop an understanding of the evolution of biodiversity. OU models of evolution were found to be the best fitting evolutionary models in explanation of the evolution of shape within *Liolaemus* when BM, OU, δ and κ models were fit. Phenotypic rate variation showed some increases in rate of evolution on PC1 whereas PC2 and PC3 showed decreases. PGLS showed a significant relationship between SVL and PC1 and for SVL and PC2 when microhabitat, parity and diet were included. Pairwise comparisons showed a significant difference between insectivorous and herbivorous species for SVL and PC1 open-ground shrubs and open ground species for SVL and PC2. The best fitting model

for PC1 and PC2 included microhabitat and diet, but not parity, for PC3 the best fitting model included diet and parity, but not microhabitat. Results suggest the lack of an ecomorphological relationship could be a consequence of other ecological factors exerting a stronger pressure on the evolution of morphology or that the adaptations are present but methodologies are not appropriate to identify them.

2 Introduction

Adaptive radiation theory predicts that lineages diversify into species that are phenotypically and ecologically distinct as a result of natural selection pushing adaptations in alternative directions (Schluter 1996; Schluter 2000; Losos & Miles 2002; Losos 2009; Pincheira-Donoso et al. 2015). Therefore, central to the concept of adaptive radiation is ecological opportunity (the origin of new biodiversity mediated by exploitation of new or previously unavailable ecological resources, Yoder et al. 2010). This process is triggered when a population accesses a new ecological domain via migration, following mass extinctions, or when a new resource within their areas of historical residence, previously unavailable, becomes available to them. A classic example of adaptive radiation is Darwin's finches, which have undergone vast diversification of morphological adaptations across the multiple islands of the Galapagos archipelago (Grant, 1986). Evidence suggests that these birds underwent diversification when the availability of several empty niches allowed ancestral species to adapt their morphology to access unexploited resources leading to the vast morphological adaptations present today (Schluter & Grant, 1984; Grant, 1986).

An intriguing outcome of the process of adaptive radiation is the replicated evolution of adaptations among less phylogenetically species exposed to similar environments, a phenomenon termed convergent evolution. Natural selection theory predicts that ecological factors can cause similar traits to evolve in distantly related species through convergent evolution (Ricklefs et al., 1981; Albert et al., 1992; Schluter, 2000; Blackledge & Gillespie, 2004; Stoks et al., 2005). Species that have evolved the similar morphological traits, specialised to use a specific structural microhabitat, as a result of convergent evolution are known as ecomorphs (Williams, 1983; Losos, 2009). *Anolis* lizards are a prime example of ecomorphological adaptations via convergent evolution. The same ecomorph classes, the groups into which they are categorized, have evolved independently on multiple islands, regardless of how shape and size is quantified, i.e. how and what variables are measured (Williams, 1983; Losos, 1992; Irschick et al., 1997; Beuttell & Losos, 1999; Losos et al., 1998, 2003; Losos, 2009). The classes are named based on the structural microhabitat they predominantly occupy - each class consists of a set of species that is morphologically, ecologically and behaviourally similar (Beuttell & Losos, 1999), resulting in six ecomorph classes: grass-bush (in bushes or on the ground in grasses), trunk-ground (on the bottom part of the trunk), trunk (in the middle of the

trunk, between trunk-ground and crown-trunk), crown-trunk (in the canopy and upper trunk), crown-giant (high in the crown of trees) and twig (in the twigs of the canopy) (Williams, 1983; Losos, 2009). Repeated exposure to the same microhabitats resulted in replicated phenotypes on the different islands, including colouration, size, body shape, perch characteristics such as height and size, and behaviours, which include but are not limited to foraging and escape behaviour. This was seemingly driven by interspecific competition between anole species to avoid resource competition (Losos, 1994, 2009). This is not an isolated occurrence. Examples of convergent evolution leading to the same ecomorphotypes as a result of exposure to the same habitat types occurs repeatedly in nature, including other lizards (Melville & Swain, 2000); bats (Aldridge & Rautenbach, 1987; Crome & Richards, 1988), bovids (Kappelman, 1988), birds (Niemi, 1985), snails (Chiba, 1999) and spiders (Gillespie, 2004).

As a result of convergent evolution when exposed to the same ecological opportunities, it has been suggested that habitat use can be predicted by morphology and vice versa (Herrel et al., 2002). For example, body shape is influenced and constrained by vegetation in lizards (Williams, 1983). Narrower surfaces and more densely vegetated habitats tend to result in narrower bodies (Pounds 1988; Losos 1990; Melville & Swain 2000; Martins et al. 2001; Herrel et al. 2002; Collar et al. 2011; Blankers et al. 2013) as narrower perch diameter and efficient movement through dense vegetation to avoid hindrance requires more streamlined morphology (Beuttell & Losos, 1999; Melville & Swain, 2000; Losos, 2009). Similarly, species that often climb on vertical surfaces, such as saxicolous and tree trunk species, tend to have broad, flat bodies (Losos 1990; Vitt et al. 1997; Aerts et al. 2000; Melville & Swain 2000; Goodman 2007; Goodman & Isaac 2008; Losos 2009; Collar et al. 2011). A similar relationship can also be found in head shape; lizard species that have short, broad, high heads occupy habitats such as tree trunks that have broad surfaces, whereas those that have narrow, long, low heads utilize narrow perches, such as twig species (Losos, 2009). As *Liolaemus* inhabit these same microhabitat types, it would be expected that they follow similar morphological patterns (Schulte et al., 2004; Pincheira-Donoso et al., 2009, See Figure 1 for Liolaemus morphological diversity and habitats).

In contrast with the above examples, accumulating evidence reveals that ecomorphs seem to have not evolved within other lineages that have undergone diversification via adaptive radiations. Interestingly, whilst convergent evolution can be found in very diverse lineages (e.g. Crome & Richards, 1988; Kappelman, 1988; Blackledge & Gillespie, 2004;

Losos, 2009), other lineages (Pincheira-Donoso et al., 2009; Vanhooydonck & Damme, 1999; Herrel et al., 2002)that exhibit extensive ecological, phenotypic and taxonomic diversity, that have evolved as a result of invasions of multiple different environments, do not seem to follow a convergent pattern linked to the known signals of natural selection. For example, in both Lacertid and Phrynosomatid lizards, some relationships between habitat and morphology have been found when using traditional non-phylogenetic methods. However, when phylogeny was taken into account, there was no evidence of ecomorphs (Vanhooydonck & Damme, 1999; Herrel et al., 2002). For Lacertid lizards it has been suggested that clustering on the phylogenetic tree may be the reason no ecomorphs were found when analysed in a phylogenetic context; Lacertids sharing similar microhabitats are closely related and thus similarities are due to a shared history rather than convergent evolution and adaptation (Vanhooydonck & Damme, 1999). Therefore, a central conclusion is that the above conditions do not guarantee the evolution of identifiable ecomorphs.

Liolaemus are remarkably diverse in morphology and environments they inhabit (Figure 1). This diversity make them an excellent model system to study adaptive radiation and the relationship between ecology and adaptation. Furthermore, they share several similarities with *Anolis*. *Liolaemus* are distributed in central-southern and southern South America (Pincheira-Donoso et al., 2007), *Anolis* have extensive radiations in Central and South America and the West Indies (Irschick et al., 1997). *Liolaemus* occupy a vast variety of habitat types, elevations ranging from sea level to over 5000m, and across several climates and latitudes, with a geographical range of more than 4500km (Pincheira-donoso et al., 2008). They range from the driest place on Earth, the Atacama Desert, to temperate *Nothofagus* rainforest, to the Patagonian steppe, the Southernmost place a lizard has been found (Schulte et al. 2000, 2003, 2004; Espinoza et al. 2004; Cruz et al. 2005; Pincheira-Donoso et al. 2007, 2008a, 2008b; Abdala et al. 2008). *Liolaemus* diets include herbivorous, omnivorous and insectivorous species (Espinoza et al., 2004) and there are both viviparous and oviparous species (Schulte et al., 2000). *Anolis* has over 300 species (Losos, 1994), *Liolaemus*' has over 240 species (Pincheira-Donoso et al., 2009). Furthermore, akin to *Anolis*, there have been multiple radiations of *Liolaemus*, each of which have occurred independently (Schulte et al. 2000; Pincheira-Donoso et al. 2008a). However, *Liolaemus* and *Anolis* do differ in some aspects such as lineage age; *Liolaemus* is between 18.5 and 20 million years old (Albino, 1998, 2008, 2011; Fontanella et al., 2012), whereas *Anolis* is estimated to be 40-66 million years old (Losos, 2009) and *Anolis*

range in size from 40-130mm (Pacala & Roughgarden, 1985) whereas *Liolaemus* size range is slightly smaller, ranging from 40-100mm (Pincheira-Donoso et al., 2011, 2015).

Previous studies addressing the relationship between *Liolaemus* multivariate morphology and the microhabitats they occupy did not find any evidence of ecomorphs (Jaksić et al., 1980; Schulte et al., 2004; Pincheira-Donoso et al., 2009). However, the studies only used linear measurements of body size and shape traits (i.e. using only trait length, two equally sized lizards can differ dramatically in body conformation), which can miss important information on shape, as identical measurements can potentially be obtained from varying shapes (Meiri, 2010; Pincheira-Donoso et al., 2011; Deeming & Ruta, 2014). Shape may also be a better indicator of the relationship between phenotype and ecological variable than size, as previous findings in Anolis lizards suggest more variation in ecological variables is accounted for by shape (Butler & Losos, 2002).

Furthermore, there is much evidence that factors other than microhabitat structure alone will drive convergent evolution. For example, dietary adaptations have been shown to result in convergent evolution of morphology (Aldridge & Rautenbach, 1987; Findley & Black, 1983; McKenzie & Rolfe, 1986; Niemi, 1985; Stayton, 2006; Hugueny & Pouilly, 1999). This would be expected as similar diets exhibit similar pressures on selection, for example, selective pressures on all herbivorous lizards are similar; they feed on items that do not need capturing, and require the ability to remove food items from a larger source (i.e. cropping part of a plant) (Stayton, 2006). Therefore, herbivorous lizards exhibit longer, wider snouts and wide heads, due to the increased bite needed to crop plants (Herrel et al., 1998, 2008; Lappin & Husak, 2005) and a large, wide body to accommodate the increased gut length needed to process plant matter (Zimmerman & Tracy, 1989) and for the warm body temperature required to digest plant material (Pough, 1973).

Additionally, a further differentiation would be expected based on parity mode, as viviparous species would need a larger abdomen to accommodate the same number and size of offspring. Females are under pressure to attain increased fecundity (Medina & Ibargüengoytía, 2010; Yang et al., 2012; Pincheira-donoso & Hunt, 2015). As the foremost prediction of the fecundity selection hypothesis (that larger body size results in higher fecundity across species) holds true in *Liolaemus* (Pincheira-Donoso & Tregenza, 2011) it would be expected that females would also evolve a body shape that increases abdominal volume (Du & Lü, 2010; Du et al., 2005; Olsson et al., 2002). Qualls & Shine (1995) found an increase in maternal SVL in with the evolution of viviparity in one species of lizard. Furthermore, viviparous females modify their thermoregulatory

behaviour to optimise temperatures for their offspring (Shine, 2006) and may benefit from a wider body to allow better absorption of heat.

To solve the longstanding problem of the relationship between the evolution of morphology in response to ecology, this study employed a more sophisticated approach: landmark-based geometric morphometrics (see Viscosi & Cardini, 2011 for a simplified overview), which accurately captures body shape in combination with the employment of molecular phylogenies. The following three hypotheses were used to investigate the interrelationship between morphology and ecology within *Liolaemus* to develop a better understanding of functional and ecological relationships:

1) Similar microhabitats promote the evolution of similar body plans. Species that occupy twigs, a habitat with a narrow surface, are expected to have a narrow, elongated body, and a long narrow head. Whereas, tree trunk species are expected to have wide bodies and short, broad heads. Likewise, saxicolous species are expected to have broad bodies. Species occupying dense vegetation, would like twig species, be expected to be narrow

   Open ground and open ground-shrub species would be expected to fall in between tree trunk and twig species, with open-ground shrub species being slightly more constrained in width due to the need to effectively move in shrubs.
2) The same diet types result in the same morphological adaptations. Herbivorous species are expected to have a wider abdomen, wider heads and wide, long snouts and insectivorous species a narrower abdomen, and shorter heads and narrower shorter snouts. Omnivorous species are expected to have an intermediate morphology between herbivorous and insectivorous species.

3) The same parity mode will cause the evolution of similar morphologies in the bodies of females, but not of males. Viviparous females are expected to have a wider, longer trunk than oviparous females; however, variation in head is expected not to differ between parity modes.

Liolaemus are also known to have high levels of sexual dimorphism (Pincheira-Donoso et al., 2009; Pincheira-Donoso & Tregenza, 2011) and are under different selection pressures, such as fecundity selection for females and optimal performance for defending territory in males (Braña, 1996; Herrel et al., 2002; Cox et al., 2003; Huyghe et al., 2005; Lappin & Husak, 2005). As such it would also be expected that males and females differ in their adaptation to the environment. It was hypothesised that:

1) Females would be wider than males to accommodate for carrying offspring and eggs. Males would be expected to show more distinct morphological groups to optimize locomotion and that males would have larger heads in proportion to body size due to male-male competition.

To further develop a better understanding the rates and patterns of body shape diversification were also explored. Phylogenetic signal is used to test if the amount similarity between species is proportional to the shared history of the taxa under Brownian Motion (BM) (Revell et al., 2008). The BM model of evolution is a random walk through time with constant variance (Pagel, 1999); the model assumes changes in trait are independent of previous change and changes on other branches, are proportional to branch length, and that evolution is constant over time (Nunn, 2011). Likewise, lambda (λ) is used to determine if traits are evolving in accordance to BM (Freckleton et al., 2002). Previous studies of *Liolaemus* morphology and size have found low phylogenetic signal (Vanhooydonck et al., 2010; Tulli et al., 2011).

The Ornstein-Uhlenbeck (OU) model of evolution, a random walk model of evolution but with stabilizing selection (Hernández et al., 2013), is used to see if evolution is being pulled towards an optimum or optima, here investigating if there are optimal body shapes in regards to microhabitat, diet or parity mode. Lack of change in a trait is not sufficient to suggest phylogenetic inertia of a trait, as it may be under stabilizing selection (Blomberg & Garland, 2002), further making OU an important model to fit to the data. The delta (δ) model is fit to determine is evolution is time-dependent (Pagel, 1999); is morphological evolution in *Liolaemus* constant, or does the rate of evolution differ in the genus' early and late evolution? A previous study found *Liolaemus* body size evolved slowly initially, followed by rapid evolution recently (Pincheira-Donoso et al., 2015). Finally, the kappa (κ) model is fit to investigate if the rate of evolution is proportional to branch length (Pagel, 1997). Studies in Anolis have found body size has evolved with accelerated evolution in long branches (Thomas et al., 2009; Thomas & Freckleton, 2012). A previous study of *Liolaemus* have found that OU is the best fitting model to explain evolution of body size (Pincheira-Donoso et al., 2015).

Analysis of evolutionary rates is used to study the evolution of morphology throughout time. This can be used to support different scenarios of evolution, such as directional selection would expect faster evolutionary rates (Rezende & Diniz-Filho, 2012).

A Phylogenetic Generalized Least Squares (PGLS) is used to investigate any relationship between shape and size, in particular within microhabitat, diet and parity categories, as

there could be adaptive morphologies, but that differ for different size groups. In Anolis lizards, for example, trunk-crown and crown giant anoles occupy similar habitats (trunks and branches) yet have distinct ecomorph classes due to differences in size (Williams, 1983; Losos, 2009). In some instances the morphology of lizards can be predicted by their size (Collar et al., 2011).

The pgls function in the R package caper (Orme, 2013) was used to determine if any correlations between size and shape were present, with and without microhabitat, diet and parity.

The following hypotheses were investigated in regard to mode and rate of evolution:

1) Phylogenetic signal would be expected to be low, as the presence of convergent evolution, such as if evolution is being driven by microhabitat type, diet or parity mode, would mean that closely related species are less similar than would be expected under BM.
2) The presence of ecomorphs in *Liolaemus*, or if evolution of *Liolaemus* morphology is being driven by diet or parity mode, it would be expected that they would follow an OU model of evolution, with either 6, 3 or 2 optima, respectively. Thus, OU would be expected to be a better fitting model than BM.
3) For the δ model of evolution, a slow initial evolution followed by rapid recent evolution is expected, as this is the pattern of evolution previously found in *Liolaemus* for body size.
4) For the κ model of evolution, proportionately higher rates of evolution in long branches is expected if ecomorphs are present, as is the case in Anolis.
5) Directional selection of morphology, as would be the case if evolution were being driven by the ecological factors being investigated, would result in faster evolutionary rates.

3 Material and Methods

3.1 Study species

Data were collected from 1121 adult *Liolaemus* specimens (510 females and 611 males) belonging to 62 species (Table 1). All samples consist of museum preserved specimens housed at the National Museum of Natural History of Chile (MNHNC), the Centro Nacional Patagonico-Puerto Madryn in Argentina (CENPAT-JAS), and the Museo de la Universidad de la Plata in Buenos Aires, Argentina (MLP). Ethanol-fixed museum specimens offer ideal opportunities to perform morphometric analyses (see below) because they can be manipulated into suitable positions to be photographed and hundreds of samples are readily available. In contrast, dried specimens show substantial alterations of body shape and proportions, and have, therefore, not been included in the analyses. Dissected, stuffed or specimens that had been otherwise altered when preserved were also excluded as their shape can be significantly altered. Each specimen was laid out flat on a light coloured surface, with the proximal portion of its legs at approximately 90 degrees to the longitudinal axis of the body and secured using pins (Figure 2), and photographed in dorsal view (at 96 dpi).

The total species sample encompasses all possible environments and geographic locations occupied by *Liolaemus* lizards in Chile, Argentina and Bolivia. These environments range from the Atacama Desert (the driest place on Earth) to the Patagonian steppe (the southernmost site where a reptile has been found), and at a wide range of altitudes in the Andes, from sea level to over 5000m (Schulte et al. 2004; Schulte et al. 2000; Pincheira-Donoso et al. 2008a). In addition, the sample covers the whole range of microhabitats in which *Liolaemus* species have been found (see below for details).

3.2 Phylogenetic tree

The phylogenetic tree upon which the analyses were based was adapted to include only the species present in this study from a comprehensive multi-gene tree of squamate reptiles (Pyron et al., 2013). The tree is calibrated based on estimates from molecular phylogenies of all *Liolaemus*' major clades (Fontanella et al., 2012) and on the fossil record of the genus (Albino, 1998, 2008, 2011). The origin of the crown group radiation, marked by the latest common ancestor of the subgenera *Eulaemus* and *Liolaemus sensu*

stricto, was set at 19.25 million years ago, as this is the midpoint of the estimated time of divergence of the two subgenera (18.5 Mya to 20 Mya), based on the aforementioned paleontological and molecular evidence. The tree was trimmed using Mesquite (Maddison & Maddison, 2011) to include only species used in this study, resulting in a tree containing 51 *Liolaemus* species (Figure 3). Details provided in Pincheira-Donoso et al. (2015).

3.3 Geometric Morphometrics Protocol

A geometric morphometrics approach was employed to address the hypotheses of a relationship between morphology and microhabitat, diet and parity mode. Shape variation was quantified across species after excluding size, translation and rotation components of biological form (see below). These techniques provide the analytical approach to discern shape changes that cannot otherwise be captured by traditional measurement methods (e.g., simple linear measurements of traits, ratios and angular measurements) and permits visualisations of shape and the locations of variation (Stayton & Ruta, 2006; Deeming & Ruta, 2014). Furthermore, which lengths and angles are important do not have to be decided before the construction of the database as in traditional morphometrics (Stayton, 2006).

The geometric morphometrics approach relies on the use of landmarks placed on high resolution pictures of the sample specimens. Landmarks are used to 'map' specimen shape by transforming samples into precise coordinates in a morphospace. Landmarks can be defined as distinct anatomical loci, identifiable in all of the specimens used in a study, and hence, all landmarks are replicated across all specimens following exactly the same sequence (Zelditch et al., 2004; Viscosi & Cardini, 2011), thus making shape comparisons between multiple specimens possible. Landmarks are digitized on each image and coordinates of the locations are extracted. The raw, unstandardized coordinates are then used in the morphometric analysis proper.

Landmarks were placed using the image processing software ImageJ (Rasband 1997-2015). The landmarks were chosen to give the best representation of overall shape, but were selected so that they could be identified and reliably placed on all specimens (Viscosi & Cardini, 2011). After visually scrutinizing shape variation and features across the lizard samples, 26 landmarks were chosen on the head and body to describe the two-

dimensional shape of the specimens (see Table 2 and Figure 2 for placement of landmarks).

A dorsal view of the lizards was used during the placing of the landmarks, as this view displayed multiple structures that can be easily identified. Additionally, some of these features could be used to help further identify head shape such as the ocular semicircle (the group of scales on the dorsal side of the head that surround the eye, landmarks 2-7, see Figure 2). Furthermore, the posterior points of the ocular semicircle (landmarks 6 and 7), as well as the landmark on the pineal eye (landmark 8), were placed on the surface of the specimen and thus help to adjust for any potential inconsistency with the orientation of the specimen. The tip of the snout was chosen because it marks the most anterior point (landmark 1). The points on the trunk between the limbs could be used to identify shape of the body (landmarks 19-22).

There are three categories of landmarks, a combination of which were used: Type 1 landmarks (e.g. landmarks 8-12, 15-18, and 23-26) are homologous points, such as the points of confluence between structures, for example, head scales. Type 2 landmarks are points such as at the minima of curvature (landmarks 13 and 14), points around a local structure (landmarks 2-7) and points equidistant from other landmarks (landmarks 19-22). Finally, extreme points (landmark 1) make up Type 3 landmarks (Zelditch et al., 2004).

Each of the landmarks, apart from the tip of the snout and the pineal eye were placed on both the left and the right side; this was to allow for an average shape to be used, thus providing better accuracy, furthermore, individual variation is beyond the scope of this investigation. Landmarks were not placed on the limbs or tail due to multiple specimens being incomplete, thus landmarks placed on these locations would not have been replicable throughout. The landmarks were saved as coordinates which were used to create a database of the specimens.

Subsequently, all coordinates of the landmarks were exported into the morphometrics software MorphoJ (Klingenberg, 2011). The specimens in this study exhibit object symmetry, meaning they are symmetrical around a median plane or axis, the left and the right side being mirror images of each other (Klingenberg & Graham, 2015). As such, this can cause statistical problems if it is not accounted for (Klingenberg et al., 2002). Object symmetry was used to obtain an average between the paired landmarks. Single landmarks (e.g. landmarks 1 and 8) are placed on the median and paired landmarks (e.g.

landmarks 11 and 12) on either side of the median axis, this is used to create an average configuration based on a combination of the entire configuration and a copy reflected to generate a mirror image, these are then entered into a Procrustes fit, which superimposes them simultaneously and combines them (Klingenberg et al., 2002; Viscosi & Cardini, 2011; Klingenberg & Graham, 2015). The use of the averaged landmarks also helps to further eliminate any potential inconsistencies due to suboptimal body positioning. The Procrustes superimposition produces an optimal alignment and average shape, removing variation due to scale, translation and rotation between the moveable and target configurations (Viscosi & Cardini, 2011; Klingenberg & Graham, 2015). This is accomplished by assigning the origin to the centroid (the point that denotes the averages of all the coordinates) of each set of coordinates to remove effects of translation. Each centroid is adjusted to give it a size of 1 to remove differences of scale. Finally, each movable configuration is rotated around the centroid until the difference between the location of the relative landmarks of the movable and target configurations is minimal to remove differences of rotation. The resulting differences in the location of equivalent landmarks must be due to variations in shape (Webster & Sheets, 2010; Klingenberg & Graham, 2015). A covariance matrix of Procrustes-adjusted coordinates was then generated across species, using all individuals, and a principal component analysis (PCA) was performed to obtain principal component (PC) scores (shape variables). PC axes used in further analyses were chosen based upon Eigenvalue scores, specifically those that explained over 10% of variation were included, as the axes that explained small amounts of variation, i.e. the higher numbered axes, are representative of noise within the data (Stayton, 2006), thus are not of biological importance and can obscure potential patterns present. Shape changes were visualized through lollipop graphs, showing the mean configuration of landmarks and the direction and magnitude of change away from the mean, as well as deformation grids which show deviation from a mean shape or between shapes by means of interpolations between landmark configurations.

3.4 Ecomorphological analyses

Theory posits that similar natural selection regimes arise in similar environments, and thus it is predicted that similar microhabitats promote evolution of similar body plans (i.e., ecomorphs: Losos 2009; Williams 1983). Ecomorph analyses were carried out to investigate the predicted effect that similar environments have on the multivariate

phenotype of species that occupy such environments, regardless of their phylogenetic relationships.

In order to manage the multiple spatial phenotypic variables returned by the geometric morphometric analysis of landmarks, we employed a Principal Components Analysis (PCA). For each species, an average shape variable was calculated along each PC axis, using the PC scores calculated from individual specimens. A mean value was calculated for males and females individually so that each sex could be analysed separately due to high levels of sexual dimorphism present in *Liolaemus* (Pincheira-Donoso et al., 2009; Pincheira-Donoso & Tregenza, 2011). To verify the presence of sexual dimorphism with the measures of morphology used in this study an NPMANOVA was carried out on male and female species averages to determine if they were significantly separated. The male and female averages were then used to calculate an overall species average to account for potential shape-bias emerging from differences in sample sizes between males and females.

Subsequently, each species was assigned a microhabitat category, based on the frequency of occurrence of individuals, using a ≥70% threshold value of the time spent by those individuals basking or dwelling whilst active (as per Pincheira-Donoso et al., 2009). Data on microhabitat category were assigned based on a dataset (Pincheira-Donoso, unpublished) and was reinforced using data from Schulte et al (2004). These categories consisted of open ground (species dwelling in open desert with little to virtually no vegetation, separated by ≥400cm when present), open ground-shrubs (species found on ground with shrubs separated by 101-400cm), ground-dense vegetation (ground species where vegetation is generally less than 100cm apart), rocks, tree trunks (primarily on trunks, rarely or never seen on twigs) and twigs (species located on shrubs) (See Table 1).

A Nonparametric Multivariate Analysis of Variance (NPMANOVA) was carried out in PAST (Hammer et al., 2001), which tests for statistical differences between groups, the test achieves this based on multiple permutations (in this case 9999 permutations) of the taxa in assigned groups, allowing for the assessment of similarities in the distribution of variances in the groups (Anderson, 2001). The test produces an *F*-value, which results from the differences between the among-group distances compared to the within-group distances. The higher the *F*-value the more likely it is that the null hypothesis, that there is no difference between groups, is false. The p value is obtained by calculating the number of F values for permutations of data randomly assigned to species ≥ the F value

of the original data when correctly assigned to species, divided by the total number of permutations (Anderson, 2001). The NPMANOVA was initially used to test the hypothesis that between species variance was greater than within species variance to ensure using averages was representative of the species and thus that individual variation does not have a substantial bearing on ecological processes and dynamics (Bolnick et al., 2003). The analysis was then used to test the hypothesis that similar microhabitats promote the evolution of similar body plans. This test was used because the data would be applicable for an ANOVA, however due to phylogenetic relatedness the data points were not independent and did not follow a normal distribution, making a non-parametric analysis essential. The analysis was performed on species, on males and females, on species' averages by microhabitat category, and on male and female averages separately by microhabitat category. To determine if any significant results were a result of similarities due to common ancestry a Phylogenetic Analysis of Variance (PANOVA) was carried out on the first PC axis and a Phylogenetic Multivariate Analysis of Variance (PMANOVA) on the first and second PC axis, and on axes one to three based on microhabitat category. This was repeated for males and females separately. These analyses was performed using R version 3.1.2 (R Development Core Team, 2014) using the package geiger (Harmon et al., 2008).

An ANOVA was also carried out in SPSS (IBM Corp., 2010) to test the hypothesis that within species variance was equal across the different microhabitat categories. Variances were calculated using Excel using the function VAR.S.

3.4.1 Phylomorphospace: An alternate analysis

A phylomorphospace plot was created based on species averages using the phylomorphospace function. This plot projects the phylogenetic tree onto the morphospace plot of first two PC axes. The plot provides an estimate of the morphology of internal nodes of the phylogeny based on the location in which the nodes are placed in the morphospace plot. Morphological node estimates are calculated based on ancestral state reconstruction. The branch lengths in the phylomorphospace plot are no longer representative of time, but distance in morphospace. The plot allows for the direction and magnitude of shape change along branches of the phylogeny to be visualised (Sidlauskas, 2008). The phylomorphospace plot was created using R version 3.1.2 (R Development Core Team, 2014) using the R package phytools (Revell, 2012).

3.5 Diet and Parity

Species were also categorized based on diet (insectivorous, omnivorous and herbivorous) and parity mode (oviparous or viviparous). Insectivorous species are defined as consuming <10% plant matter, omnivorous species consumed 11-50% plant matter, and herbivorous species consumed 70-100% plant matter (as per Espinoza et al., 2004). Viviparous species exclusively give birth to live young, oviparous species exclusively lay eggs. Categories were assigned based on information from Pincheira-Donoso et al. (2008), aside from for *Liolaemus shehuen* which was obtained from Abdala et al. (2012) and diet categories for *Liolaemus manueli*, *Liolaemus morenoi* and *Liolaemus paulinae*, which were from a dataset (Pincheira-Donoso, unpublished). An NPMANOVA was used again to first test the hypothesis that species that consume the same diet would be morphologically similar, then to test the hypothesis that species that share a parity mode are morphologically similar. As before, the analyses were performed on species' averages and on male and female averages separately. Furthermore, whilst it would not necessarily be expected for there to be a difference between head shape between different parity modes, it cannot be disregarded, as there may, for example, be biological constraints due to live birth. As such analyses were further separated into head only and body only, to do this morphometric analyses were performed on these variables. These were carried out as above except for the head, landmarks 13-26 were omitted, thus including landmarks from the tip of the snout up to, and including, the landmarks placed at the ear openings. For the body, landmarks 1-12 were omitted, which caused the numbering of landmarks to shift so that landmark 13 became landmark 1, 14 became landmark 2, and so on. Species, male and female averages were again used to run an NPMANOVA for head only analysis and body only analysis. As before these were each analysed in a phylogenetic context.

3.6 Mapping of phylogenetic traits

Microhabitat, diet and parity mode were mapped onto the phylogenetic tree using the function tiplabels, enabling the distribution of traits to be observed on the phylogeny. Thus allowing the location of specific traits and their proximity to species in the same category to be visualised on the tree, without which the interpretation of results pertaining to convergent evolution would be difficult. The mapping of traits was carried out in R (R Development Core Team, 2014), using the package Ape (Paradis et al., 2004).

3.7 Phylogenetic Analyses of Shape Evolution

Phylogenetic macroevolutionary analyses were used to examine shifts and rates of character evolution during the history of *Liolaemus*. These analyses are vital to the understanding of the evolution of biodiversity; as to understand what external factors are affecting evolution, that which is explainable by relatedness needs to be taken into consideration. Furthermore, different processes of evolution can be supported through the analysis of evolutionary rates (Rezende & Diniz-Filho, 2012). All analyses were carried out using species averages, and male species average and female species average individually. For each analysis 51 species were included, aside from parity mode analysis where only 50 were included, and were performed on the first three principle component axes.

The function phylosig in the R package phytools (Revell, 2012) was used to calculate phylogenetic signal on Blomberg's *K*. Phylogenetic signal is defined by Revell et al. (2008) as 'the statistical nonindependence among species trait values due to their phylogenetic relatedness.' If phylogenetic signal is low it suggests that closely related species do not resemble each other and therefore phylogenetic statistical modelling methods may not be required as the data points can be considered independent (Blomberg et al., 2003). Under a BM model of evolution (a random walk model with constant variance, used for traits that vary naturally along a continuous scale) the amount of variance expected at the tip for the given trait is proportional to the shared history of the taxa and as such can be used as a reference model. Phylosig produces a *k* value, Blomberg's *K*, which, when <1 it suggests that there is less resemblance than expected under BM, while values above one indicate a greater such similarity. The *k* value was compared to 1 by generating a null distribution where $k = 1$ and counted the number of times the simulated *k* values were more extreme than the reported *k* values. However, using phylogenetic signal to infer evolutionary processes is not feasible (Revell et al., 2008) and thus further methods need to be applied.

The fitContinuous function in the R package geiger (Harmon et al., 2008) was used to fit the λ model to the data, which is similar to phylosig in function. λ is used to determine if traits evolve in accordance to expected covariance (Hernández et al., 2013). A λ value of 0 means evolution of the trait is entirely independent of phylogeny, a value of 1 means the trait evolves as would be expected in a BM model, a value greater than 1 indicates the traits of species are more similar than would be expected under BM (Freckleton et al., 2002). λ values were tested to see if they were significantly different from when λ is

forced to be 1 and forced to be 0 using a likelihood ratio (LR) test (LR=-2*(log-likelihood of better fitting model)-(log-likelihood of worse fitting model)), significance was calculated against a χ^2 distribution.

The fitContinuous function was then used to carry out model fitting; the function allows various models of character evolution to be fitted to phylogenetic trees. The models describe different evolutionary processes and as such allow the likeliest model of evolution to be identified. This provides an understanding of what process was likely in place for the evolution of shape in the dataset, as well as informing whether the majority of character changes took place early or late in the tree. This information can help to form an understanding of factors that affect the evolution of shape and if they correspond to the variables of interest in this study. BM; OU with a single optima, δ and κ models were fit to the data. OU shows stabilizing selection; like BM, OU is a random walk through time but with an optimum, or central value; as evolution causes the trait to change from the optimum, it is pulled back, the strength of this restraining force is shown by the alpha (α) value and is proportional to the distance of the trait from the optimum (Nunn, 2011). δ is a time dependent evolutionary pattern, it accomplishes this by rescaling the length of the paths, a δ value <1 suggests rapid initial evolution followed by slower evolution i.e. and early burst, a value of 1 shows constant, gradual evolution, a value >1 suggests slow initial evolution with recent evolution being fast, a δ value of 0 means amount of evolution of the trait is independent of path lengths (Pagel, 1999; Hernández et al., 2013). κ scales the lengths of branches to inform about the gradualism of evolution, a κ value of 1 means trait evolution is directly proportionate to branch length, a value of <1 means that longer branches are disproportionately shortened, a value of >1 means that there is proportionately more evolution in longer branches, a κ value of 0 means that trait evolution is independent of branch length (Pagel, 1997, 1999; Hernández et al., 2013).

The best model was selected by comparing the maximum likelihood fit (the model that is most likely to produce the data being assessed) through the Akaike Information Criterion (AIC) values, which balance how good the fit is against how complex the model is (Hunt & Carrano, 2010). The best fitting model was compared to the second best fitting model using an LR test and significance was calculated against a χ^2 distribution.

As the fitContinuous function does not allow for the fitting of multiple optima to the OU model, and as it would be expected that either two, three or six optima would be present if morphological evolution was being pushed by parity mode, diet or microhabitat

respectively, the OUCH (Butler & King, 2004) package was used to fit multiple optima. The same criteria were used to assess the models as for the fitContinuous models.

The R package motmot (Thomas & Freckleton, 2012) was used to examine shifts in evolution. The transformPhylo.ML function fits models using maximum-likelihood assessment; the trait medusa 1 algorithm ("tm1" model) was used, which fits a BM model to the data. It then fits a two-rate model at each node, where two different evolutionary rates are applied to the branches, in all possible combinations. The best model is chosen based on AIC values. The traitMedusaSummary function, also in motmot, summarises the output of transformPhylo.ML thus summarizing phenotypic rate variation on the phylogeny. The tree was then plotted using the plotPhylo.motmot function that adds colours based on the rates of trait evolution. The resulting tree can be used to identify higher evolutionary rates, visualised by longer branches, and evolutionary rates that are lower than expected, identifiable by shorter branch lengths. Knowledge of ecology of the species, such as microhabitat, can then be applied to easily determine by visual means if there is a potential relationship between rate of evolution and any factors of interest.

The pgls function in the R package caper (Orme, 2013) was used to determine if any relationships were present between size and shape, with microhabitat, diet and parity as factors. Whilst scale is removed from PCA by a Procrustes superimposition, no information on allometry is provided, thus species of a particular body size may occupy a specific region of morphospace and as such differences in body size could cause convergence of morphologies (Stayton, 2006). The function calculates a regression between continuous variables taking into account phylogenetic relatedness. This function was used to test for a relationship between shape and size; snout vent length (SVL) was used as a measure of size. SVL was obtained for as many individuals as possible, from which an average was obtained such as that for the PC scores; an average was calculated for the males and the females and then from this an overall species average was calculated (see above for further details). A PGLS regression was carried out on PC1 through to PC3, each with log transformed SVL. Log transformation was carried out on SVL to reduce skew and homogenize variances. A PGLS regression was then carried out on PC1-3 with microhabitat, diet and parity as factors. For models that returned a significant result, pairwise comparisons were carried out to determine which categories were significantly different. P values were adjusted using false discovery rate (fdr) correction to account for multiple tests being carried out. The PGLS regression was then repeated with one variable removed each time and the best fitting model selected based on AIC.

Analyses were performed using R version 3.1.2 (R Development Core Team, 2014).

4 Results

4.1 Distribution of Body Shapes in Morphological Space

There was a large overlap between *Liolaemus* species within morphospace (Figure 4). However, species were significantly separated in body shape (NPMANOVA: On all specimens using PC1 and PC2; $F_{61,1059}=11.79$, $P=0.0001$, Appendix), as such between-species variation in body shape was greater than within-species variation. As individual variation was beyond the scope of this study, greater variation between species indicates that averages were a sufficient means of representing body plans for species. Whilst some species (such as *L. paulinae* for PC1) show vast amounts of intraspecific variation (Figure 5), the overall within-species variation for each microhabitat group was not significantly different (ANOVA: Variance of microhabitat groups using PC1-3, $F_{56,61}=1.207$, $P=0.318$).

4.1.1 Morphometric analysis

The morphology of a species can be determined by its location in morphospace. The associated changes in morphology with each PC axis are described below to give an understanding of the location and direction of change for each axis.

4.1.1.1 Entire specimen

The first PC axis, which summarizes 33.10% of variance across species (Table 3), describes variation of overall head shape, with change occurring at all landmarks of the head, except from the ears which remain virtually unchanged, as the size of the head in relation to the body decreases, the size of the body in relation to the head increases and vice versa (Figure 6a). A low PC1 score shows a reduction in head size in relation to body size overall; there is a shortening and slight narrowing of the snout, and an anterior shift of the neck, converging on the landmarks indicating the ears. There is a widening and lengthening of the trunk, as both the forelimbs and hind limbs move anteriorly and posteriorly respectively. Specimens with a high PC1 score show a narrowing and slight shortening of the trunk, a lengthening of the snout and a lengthening and narrowing of the neck.

PC2, which explains 25.24% of variation (Table 3), overall shows changes laterally, in particular of the trunk and neck. There is very little change in the head, only a slight shift

occurs at the cheeks, ears and a very small displacement at the outer points of the ocular semicircle (landmarks 4 and 5). There is also a change in the length of the body as the hind limbs and forelimbs move in opposing directions to achieve a lengthening or converge resulting in a shortening (Figure 6b). A high PC2 score shows a general narrowing overall, a slight inwards shift occurs at the cheeks and ears and a very small inwards displacement at the outer points of the ocular semicircle. There is also a slight lengthening of the trunk as the hind limbs shift to the posterior and the forelimbs move slightly to the anterior. Those with a low PC2 score exhibited a widening and a slight shortening of the trunk.

In PC3, which explains 10.44% variation (Table 3), as the rear of the trunk increases in size, the front decreases and vice versa (Figure 6c). Variation also occurs around the snout. A low PC3 score indicates an anterior shift in the trunk, towards the front limbs and a simultaneous shift posteriorly of the hind limbs, resulting in a lengthening of the rear of the trunk, the forelimbs virtually do not move, thus there is a pinching at the front of the trunk. There is an enlargement of the snout and head and a posterior shift of the head and neck towards the forelimbs. Thus a high PC3 score indicates a decreased posterior region of the trunk and increased anterior region, whilst the snout and head shows a decrease in size, both shortening and narrowing.

The first three principal component axes were selected for analysis to be performed on as these were the axes that explained over 10% of variance. Cumulatively they summarize 68.78% of variance in eigenshape analysis (Table 3, Figure 7).

4.1.1.2 Head Only

The first axis, which summarizes 25.93% of variation (Table 4), shows a decrease in size at the rear of the head as the snout becomes more elongated and an increase when the snout becomes shorter. There is a slight shift in the relative position of the ears, but the majority of change takes place at the snout (Figure 8a). A high PC1 score shows a decrease in size at the rear and an elongation of the snout. There is a slight shift inwards and anteriorly of the ears and the tip of the snout moves forward whilst the pineal eye moves back. There is a general enlargement of the ocular semicircle; however, there is only a slight shift towards the anterior and outwards, the majority of change takes place posteriorly. The cheeks move forward and inwards slightly, decreasing the size of the region between the ocular semicircle and the wider point of the cheek. A low score results in a shorter snout and larger region in the back of the head.

Conversely along PC2, which explains 24.81% of the variation (Table 4), the majority of change occurs at the back of the head (Figure 8b). A low PC2 score indicates that the ears move outwards and forwards and the cheeks move outwards but not forwards, the posterior of the ocular semicircle moves backwards and slightly outwards, thus there is a shortening but widening to the back region of the head. Again the ocular semicircle becomes larger, but this is only slight, the back and outer points (landmarks 4, 6, 5 and 7) move back and outwards slightly, while the front points remain unchanged. The tip of the snout moves back slightly, but there is no variation in length of snout as the amount is approximately equal to that which the pineal eye shifts back by. A low PC2 score indicates a smaller posterior region of the head.

PC3 (Figure 8c) explains 18.11% of the variation (Table 4). As in PC2, the majority of change occurs around the back of the head; it widens as it lengthens, and becomes narrower as it becomes shorter. The pineal eye does not displace and there is only slight change in the snout. The front of the head decreases in size with a low PC3 score. The tip of snout and the points at the ocular semicircle all move inwards slightly. The ear openings move backwards and outwards and the cheeks forwards. A high PC2 score exhibits a smaller region of the back of the head, and a larger anterior region of the head.

The fourth axis (Figure 8d) explains 11.44% of the variation (Table 4). The majority of change occurs within the snout rather than the back of the head. Again the pineal eye does not move. A high PC4 score indicates the snout becomes shorter as the tip of the snout moves posteriorly, a widening also occurs as the outer and posterior points of the ocular semicircle move outwards The cheeks move forwards and inwards causing a pinching in the region between the outer point of the cheek and the posterior region of the ocular semicircle. The ears move inwards and backwards slightly; as such the back region of the head is slightly enlarged. A low PC4 score results in a decreased posterior region of the head and a longer but narrower snout.

The first four principal component axes were selected for analysis to be carried out on as these were the axes that explained over 10% of variance; cumulatively they summarize 80.29% of variance in eigenshape analysis (Table 4, Figure 9).

4.1.1.3 Body Only

The first axis, which summarizes 41.88% of variation (Table 5), mostly only shows lateral variation, though there is some anterior and posterior displacement of the limbs (Figure 10a). A low PC1 score shows a general narrowing along with an elongation of the trunk

as the forelimbs shift anteriorly slightly and the hind limbs shift posteriorly. A high score on PC1 results in a wide and slightly shortened body.

PC2, which explains 16.55% of the variation (Table 5), also shows lateral displacement but only in the trunk, particularly in the posterior region, the hind limbs remain virtually unchanged whereas the forelimbs and the neck show anterior or posterior displacement (Figure 10b). A low PC2 score shows a narrowing, the trunk becomes shorter as it narrows, however the neck becomes longer as the forelimbs move posteriorly and the landmarks on the neck simultaneously move anteriorly. A high PC2 score results in a widening and elongation of the trunk and a shortening of the neck.

PC3 on the other hand, which explains 14.87% of the variation (Table 5), only shows very slight variation laterally, most of the displacement occurs anteriorly or posteriorly. The neck remains unchanged (Figure 10c). A low PC3 score exhibits an enlarged posterior region of the body and a shortening and narrowing of the anterior region as the forelimbs shift anteriorly and the hind limbs posteriorly and also slightly outwards. Conversely a high PC3 score results in an increased posterior region and a decreased anterior region of the body.

The axes that explained over 10% of variance and were thus selected for analysis to be carried out on were the first three. Cumulatively they summarize 73.30% of variance in eigenshape analysis (Table 5, Figure 11).

4.2 Ecomorph Analysis

The ecomorphological analysis did not show distinct groups based on microhabitat. Body shapes did not follow a predictable pattern as expected by convergent evolution in regards to microhabitat. The open ground-shrub microhabitat group occupied a large amount of the morphospace (Figure 12a). Ground-dense vegetation species, which are located centrally, to the right in morphospace, almost entirely overlapped with the open ground-shrub group. There is also a large amount of overlap between rock, located centrally and to the left, and open ground-shrub species. There is only one species which occupies twigs and this species is located within the area occupied by the open ground-shrub group, towards the top right of the morphospace. The two tree trunk species are located in the left central part of morphospace and one species occurs within the open ground-shrub and rock species while the other is not located within any of the other microhabitat groups.

The NPMANOVA test showed significant separation between open ground and open ground-shrubs (NPMANOVA: Species averages; PC1 and PC2; $F_{5,56}$=3.944, P=0.0308) and between open ground-shrubs and tree trunks (NPMANOVA: Species averages, PC1 and PC2; $F_{5,56}$=3.853, P=0.0348) when overall species averages were used. There was also a relatively large overlap between ground-dense vegetation and rock species, other groups showed little or no overlap, but were not significantly separated. However, when phylogeny was accounted using PANOVA and PMANOVA for there was no significant separation between microhabitat groups (Table 6).

Females largely tended to occupy the right side of the morphospace, and males the left (Figure 12b) and as such females tended to have a higher PC1 and PC2 value than males of the same species meaning females were characterized by a narrower, shorter trunk, a longer snout, and a longer but narrower neck in relation to males. Males and females were significantly separated across species in morphospace (NPMANOVA: Female and male species averages, PC1 and PC2; $F_{1,118}$=101.6, p=0.0001). Furthermore, there was significant separation between males and females that occupied the open ground-shrub microhabitat (NPMANOVA: Female and male species averages, PC1 and PC2; $F_{11,109}$=13.97, p=0.0001). There was no significant difference between microhabitat groups when female averages were analysed separately and only for the open ground-shrub and tree trunk groups in males (NPMANOVA: Female species averages, PC1 and PC2; $F_{5,56}$=3.906, p=0.0297). When phylogeny was accounted for using PANOVA and PMANOVA there was no significant separation between microhabitat groups for both males and females (Table 6).

4.2.1 Phylomorphospace

The phylomorphospace (Figure 13) showed no clear patterns. Some species that are not closely related but occupy the same part of the morphospace and share the same microhabitat (e.g. *L. paulinae* Figure 13, no. 46 and *L. koslowskyi* Figure 13, no. 2). Other species that are closely related but occupy different areas of the morphospace and different microhabitats (e.g. *L. chiliensis* Figure 13, no. 37 and *L. pictus* Figure 13, no. 36). However, there are no distinct clusters of species within the morphospace based on microhabitat, and species that occupy the different microhabitats overlap in morphospace.

4.3 Diet-related Analysis

Herbivorous and insectivorous species evolved differing body plans to adapt to the differing associated demands, omnivorous species evolved an intermediate morphology. Thus morphology can be at least somewhat predicted based on expectations from convergent evolution in regards to diet type.

Both insectivorous and omnivorous species overlapped greatly, occupying the majority of the morphospace when using species averages (Figure 14a), resulting in non-significant differentiation between the two groups (NPMANOVA: Species averages, PC1 and PC2; $F_{2,59}=1.751$, $P=0.1789$). Herbivorous species were located in the bottom right corner of morphospace, meaning they had a high PC1 score and a low PC2 score. Herbivorous species were significantly different from insectivorous species (NPMANOVA: Species averages; PC1 and PC2; $F_{2,59}=4.376$, $P=0.0221$) but not from omnivorous species (NPMANOVA: Species averages; PC1 and PC2;, $F_{2,59}=1.761$, $P=0.1768$). When using male and female averages the females were located to the top right and the males to the bottom left (Figure 14b) and generally followed a similar pattern to species averages. Again herbivorous species were located in the bottom right for both males and females, however males were more constrained than females, and male herbivorous species were significantly separated from male insectivorous species (NPMANOVA: Male species averages; PC1 and PC2; $F_{2,59}=4.87$, $P=0.0157$), as were herbivorous females from insectivorous females (NPMANOVA: Female species averages; $F_{2,55}=3.818$, $P=0.0349$). Male insectivorous species were also significantly separated from omnivorous species (NPMANOVA: Male species averages; $F_{2,59}=3.463$, $P=0.0372$), this may be as male omnivorous species were confined to the centre of morphospace, whereas male insectivorous species tended to have a lower PC1 score and varied from a very high to a very low PC2 score. This was not the case for females (NPMANOVA: Female species averages; $F_{2,55}=1.899$, $P=0.1597$), as females overlapped a lot more for these groups. For both males (NPMANOVA: Male species averages; $F_{2,59}=1.665$, $P=0.1933$) and females (NPMANOVA: Female species averages; $F_{2,55}=1.338$, $P=0.2607$) herbivorous and omnivorous species were not significantly separated. There was no significant separation between dietary groups for species averages, males or females when phylogeny was taken into account using PANOVA and PMANOVA (Table 6).

4.4 Parity mode-related Analysis

Overall body shape differs between viviparous and oviparous species. Morphology of only the body of females also differs between parity modes, however, this is not the case for males when body is investigated separately, or for head morphology.

Oviparous and viviparous species both occupied the central region of morphospace when using species averages (Figure 15a). However, oviparous species tended to extend more up and down the PC2 axis whereas viviparous species tended to extend more across the PC1 axis and as such were significantly separated (NPMANOVA: Species averages; $F_{1,60}=5.138, P=0.0081$). The same pattern held true for males and females, although females were located more to the top right region of morphospace in relation to the males. Additionally, female viviparous species were considerably less constrained to a specific region of morphospace and female oviparous species were constrained to a greater extent (Figure 15b). Both males (NPMANOVA: Male species averages; $F_{1,60}=4.352, P=0.0169$) and females (NPMANOVA: Female species averages; $F_{1,56}=4.7, P=0.0123$) of the different parity modes were significantly different.

The two parity modes overlap almost entirely within morphospace when only the heads are used using species averages (Figure 16a) and are as such not significantly separated (NPMANOVA: Species averages; $F_{1,60}=1.653, P=0.1983$). This is also the case for males and females (Figure 16b), not only do males and females overlap substantially (NPMANOVA: Male and female species averages; $F_{1,118}=1.809, P=0.1749$), but male oviparous and viviparous species also do (NPMANOVA: Male species averages; $F_{1,60}=1.631, P=0.2003$), as do females of the different parity modes (NPMANOVA: Female species averages; $F_{1,56}=2.023, P=0.1347$).

When only body shape was taken into account, oviparous and viviparous species still occupied the central region of morphospace using species averages (Figure 17a), as when the entire specimen was used. However, while oviparous species still extended up and down the second PC axis, they also extended as far down the first PC axis as the viviparous species. However, the viviparous species did not extend up and down the PC2 axis but did extend further up the PC1 axis than oviparous species. Furthermore, the two were not significantly separated (NPMANOVA: Species averages; $F_{1,60}=2.569, P=0.0926$). Males followed the same pattern but were less constrained (Figure 17b) and were also not significantly separated (NPMANOVA: Male species averages; $F_{1,60}=2.61, P=0.0847$). Females however followed a different pattern (Figure 17b), viviparous

species ranged from a low to high PC1 and PC2 score, whereas oviparous species remained central on the second PC axis but ranged from a low to very high PC1 score. Female oviparous and viviparous species were significantly different in body shape (NPMANOVA: Female species averages; $F_{1,56}$=4.575, P=0.0164). There was no significant separation between parity modes in any instance when phylogeny was taken into account (Table 6).

4.5 Patterns of Evolutionary Diversification of Body Shape

The distribution of microhabitat, diet and parity on the phylogenetic tree (Figure 18) shows some areas where clustering of traits occurs, however, there are also clades which show varied traits.

4.5.1 Phylogenetic Signal

For PC1-3 phylogenetic signal was low and *K* was significantly different to 1 (Phylosig: Blomberg's *K*; PC1, k=0.336, p=0.0050; PC2, k=0.374, p=0.0070; PC3, k=0.277, p=0.0010) suggesting that there is significant departure from BM, therefore there is less similarity between related species than would be expected. Circumstances that cause evolution to deviate from BM, such as adaptation, can cause low phylogenetic signal, as can many other factors, including errors in measurement and phylogeny (Blomberg & Garland, 2002). For λ, PC1-3 and SVL were significantly different from 1 and 0 (fitContinuous; SVL, λ=0.899, p(λ=0)<0.0001, p(λ=1)=0.0165; PC1, λ=0.466, p(λ=0)=0.0002, p(λ=1)<0.0001; PC2, λ=0.767, p(λ=0)=0.0021, p(λ=1)=0.0003, PC3, λ=0.544, p(λ=0)=0.0060, p(λ=1)<0.0001, Table 7). This suggests that there is significant departure from BM, but species were also not independent of phylogeny. However, using Blomberg's *K* SVL was not significantly different from 1 (SVL, k=0.584, p=0.1528) suggesting that there is not significant departure from BM.

Inferences of evolutionary processes cannot be made based on tests for phylogenetic signal, thus the fitting of various evolutionary models was tried to gain more information about evolutionary processes, as suggested by Revell et al (2008). Furthermore, the presence of phylogenetic signal, or the lack there of, is not an adequate means of determining if phylogenetically controlled statistical tests are necessary (Revell, 2010), thus phylogenetic tests were employed as well as non-phylogenetic methods.

4.5.2 Models of evolution

4.5.2.1 Body Size

Body size (SVL) is identified to follow the δ evolutionary model (fitContinuous function, Table 8); as such size follows a time-dependant evolutionary pattern. As the value of δ was >1 (δ = 2.999) it suggests that recent evolution has been relatively fast. However, this is not a significantly better fit than OU (α=0.102; chi square: δ vs. OU maximum likelihood, df=1, P=0.497). This model shows stabilizing selection; it is a random walk but with a selective optimum and thus direction towards a point, which is the result of stabilizing selection pulling the phenotype toward a phenotypic optimum. The OU model of evolution coincides with the low value shown for phylogenetic signal as stabilizing selection can remove the resemblance between ancestors and their descendants (Blomberg et al. 2003). Furthermore, the OU model is potentially indicative of convergent evolution, suggesting that there may have been external influences present that were shaping evolution rather than phylogenetic factors. The κ value was <1 (κ=0.669), suggesting there is proportionately less evolution in longer branches.

When multiple optima were included for OU, 3 optima showed the best fit (hansen test, α=4.289, Table 9) out of 1, 2, 3 and 6 optima. 3 optima was a significantly better fit than the second best fit of 6 optima (hansen test, α=3.303, Table 9, chi square: OU 3 optima vs. OU 6 optima maximum likelihood, df=1, P=0.0011) and a significantly better fit than the δ model of evolution (chi square: OU 3 optima vs. δ maximum likelihood, df=1, p<0.0001). The optima for the best fitting model were 4.00176, 4.34136, 4.05622.

SVL shows an increase in *L. scolaroi* in phenotypic rate variation (Figure 19).

4.5.2.2 Body Shape

Evolution of shape is best explained by the OU model according to the fitContinuous function, suggesting that body shape evolution moves toward an optimum, as results showed the best fit by both maximum likelihood and AIC for PC1 (α=0.193; Table 8) and PC2 (α=0.172; Table 8) and is a significantly better fit than the second best fit of δ (δ=2.999) for PC1 (chi square: OU vs. δ likelihood, df=1, p=0.0170). However, the second best fit for PC2, δ (δ=2.999) is not a significantly better fit than OU (chi square: OU vs. δ likelihood, df=1, p=0.0869).

PC3, fits the κ model (κ=0.000) of evolution best (Table 8), as the κ value is 0 is suggests that evolution is punctuational, however, this is not significantly better than the second best fit model, OU (α=2.399; chi square: κ vs. OU maximum likelihood, df=1, P=0.0912).

The κ model for PC1 (κ=0.299) and PC2 (κ=0.442) was <1, suggesting proportionately less evolution occurred in longer branches. δ was consistently >1 (PC1, 2 and 3: δ=2.999) suggesting body morphology evolved slowly initially, followed by rapid evolution in recent history.

However, when multiple optima were included using OUCH, OU with 6 optima was the best fitting model (Hansen test, Table 9), for PC1 (α=16.056), PC2 (α=3.508) and PC3 (α=11.530). OU with 6 optima was a significantly better fit for PC1 compared to the second best fit of 3 optima (chi square: OU with 6 optima vs. OU with 3 optima maximum likelihood, df=1, *p*=0.0031) and than the best fitting model found using fitContinuous (chi square: OU with 6 optima vs. OU with 1 optima maximum likelihood, df=1, *p*=0.00004). OU with 6 optima was a significantly better fit for PC2 compared to the second best fit of 3 optima (chi square: OU with 6 optima vs. OU with 3 optima maximum likelihood, df=1, *p*= 0.0004) and than the best fitting model found using fitContinuous (chi square: OU with 6 optima vs. OU with 1 optima maximum likelihood, df=1, *p*=0.0003). OU with 6 optima was a significantly better fit for PC3 compared to the second best fit of 3 optima (chi square: OU with 6 optima vs. OU with 3 optima maximum likelihood, df=1, *p*= 0.0078) and than the best fitting model found using fitContinuous (chi square: OU with 6 optima vs. κ maximum likelihood, df=1, *p*=0.0011).

The optima for PC1 found by the best fitting model were 0.00453, -0.00379, 0.00563, -0.01989, -0.03080, 0.01336. For PC2 the optima were -0.03605, 0.00246, 0.00758, 0.01500, 0.00559, 0.05075. For PC3 the optima were 0.00858, -0.00213, -0.00401, 0.00417, 0.00721, 0.00167.

Phenotypic rate variation on PC1 showed an increase in rate of evolution compared to what is expected in *L. kriegi, L. elongatus, L. leopardinus, L. buergeri, L. ceii* (Figure 20). This group consists of two open ground-shrub and three rock species. All species are viviparous and omnivorous.

PC2 shows a decrease in rate of evolution compared to what is expected in *L. paulinae, L. zapallarensis, L. nitidus, Liolaemus nigroviridis, L. lemniscatus* and *L. tenuis* (Figure 21). Surprisingly this group encompasses four of the six microhabitats. This decrease compared to what is expected may suggest that the radiation into different microhabitats does not involve large amounts of diversification of shape to enable species to adapt to the habitats. It also includes both oviparous and viviparous species and omnivorous and insectivorous species.

PC3 shows a decrease in rate of evolution compared to what is expected in *L. irregularis*, *L. koslowskyi*, *L. darwinii* and *L. grosseorum* (Figure 22). These species are all open-ground shrub species, so if there is a relationship between microhabitat and morphology it may be expected for a reduction in the evolution of shape to be seen if there is no radiation to other microhabitats. Apart from *L. irregurlaris*, which is omnivorous and viviparous, all species are insectivorous and oviparous.

4.5.3 Body Size and Body Shape Regression Analysis

There was a significant correlation based on the pgls function between PC1 and SVL (PGLS: PC1 and SVL; $F_{1,49}$=8.825, p=0.004594, R^2=0.1526, Table 10) however, the independent variable explains an extremely low amount of variance. SVL is not correlated to PC2 (PGLS: PC2 and SVL; $F_{1,49}$=1.414, p=0.2402, R^2=0.02804, Table 10) or PC3 (PGLS: PC3 and SVL; $F_{1,49}$=0.1459, p=0.7006, R^2=0.003043, Table 10).

When microhabitat, parity and diet were included as factors the strength of the correlation increased for PC1 and SVL (PGLS: PC1 and SVL with microhabitat, diet and parity; $F_{9,40}$= 3.911, p=0.0013, R^2=0.468, Table 10). However, pairwise comparisons with fdr corrected p values showed no significant differences between any microhabitat categories on PC1 when controlling for SVL, viviparous species were not significantly different to oviparous species (PGLS: viviparous vs oviparous; p=0.7937). Pairwise comparisons found no significant differences between omnivorous species and herbivorous or insectivorous species (PGLS: Omnivorous vs insectivorous; fdr corrected p=0.9902, herbivorous vs omnivorous, fdr corrected p=0.3662), but did find a significant difference between insectivorous and herbivorous species (PGLS: Insectivorous vs herbivorous; fdr corrected p=0.0031, Figure 23).

PC2 and SVL becomes significant when microhabitat, diet and parity are included (PGLS: PC2 and SVL with microhabitat, diet and parity; $F_{9,40}$=3.23, p=0.0049, R^2=0.421, Table 10). Again, pairwise comparisons with fdr corrected p values showed no significant differences between any microhabitat categories on PC2 when controlling for SVL, aside from for open-ground shrubs and open ground species (PGLS: Open-ground shrubs and open ground; fdr corrected p=0.0347, Figure 24) and viviparous species were not significantly different to oviparous species (PGLS: viviparous vs oviparous; p=0.4730). Pairwise comparisons found no significant differences between any dietary categories (PGLS: Omnivorous vs insectivorous; fdr corrected p=0.6601, herbivorous vs

insectivorous; fdr corrected p=0.1427, herbivorous vs omnivorous; fdr corrected, p=0.1427).

The result remained non-significant for PC3 and SVL (PGLS: PC3 and SVL with microhabitat, diet and parity; $F_{9,40}$=1.028, p=0.435, R^2=0.188, Table 10) when factors were included.

However, based on AIC, the best fitting model for PC1 and PC2 included microhabitat and diet, but not parity (PC1, model 5: AIC=-291.3466; PC2, model 5: AIC=-280.48, Table 11). The best fitting model for PC3 included diet and parity but not microhabitat (PC3, model 3: AIC=-334.3322, Table 11).

4.6 Summary

Liolaemus species are significantly separated despite, based on visual scrutinization of the morphospace plot, there appearing to be a lot of overlap (Figure 4). Within-species variation for each microhabitat group is not significantly different. Three Principal Component (PC) axes were chosen for analyses of the entire specimen, summarizing a total of 68.78% of variance. The first four axes were chosen for the head only, summarizing 80.29% of variance, and the first three axes for the body only, explaining 73.30%. Males and females were significantly separated across species in morphospace based on the entire specimen and the body but not for the head. There was little morphological variation between microhabitat groups. Morphological differences are apparent between different dietary groups, though the extent differs. Morphological differences were observed between parity modes in females based on analysis of the body. However, no results were significant when phylogenetic relatedness was considered. Phylogenetic signal was consistently low. An OU model of evolution with 6 optima was found to be the best fitting model for PC1, PC2 PC3 and an OU model with 3 optima was obtained for SVL. PC1 and SVL showed some increases in rate of evolution where as PC2 and PC3 showed decreases. PGLS showed a significant relationship between SVL and PC1, but not for SVL and PC2 or SVL and PC3. When microhabitat, parity and diet were included, SVL and PC2 became significant. Pairwise comparisons showed a significant difference between insectivorous and herbivorous species for SVL and PC1 open-ground shrubs and open ground species for SVL and PC2. The best fitting model for PC1 and PC2 included microhabitat and diet, but not parity. The best fitting model for PC3 included diet and parity but not microhabitat.

5 Discussion

This research provides a novel analytical angle to address the hypothesis that multivariate ecomorphological adaptations are driven by convergent natural selection across similar microhabitats. The hypothesis of convergent evolution has been extensively tested and supported in a range of different lineages (Niemi, 1985; Aldridge & Rautenbach, 1987; Crome & Richards, 1988; Kappelman, 1988; Melville & Swain, 2000; Gillespie, 2004; Losos, 2009). However, a number of studies conducted in other groups have failed to identify evidence for convergent evolution. The exceptionally prolific *Liolaemus* lizard radiation being one of the exemplary cases in which microhabitat-based convergent evolution has not been detected. Here an approach that quantifies body shape (geometric morphometrics) rather than linear measures used in previous studies (in which two specimens, generating the same measures for the length and the width of the trunk, for example, can still differ in shape) was used. This approach found corroborating evidence that *Liolaemus* body plans generally do not conform to expectations of ecomorphological theory. By using a more direct approach to measure phenotypic responses to natural selection, these findings reiterate the questions whether ecomorphological adaptations at the body shape level are the norm in some lineages while not in others, and whether other components of the phenotype can inhibit adaptations which otherwise may lead to convergent natural selection (Huey et al., 2003).

5.1 Natural Selection in Response to Microhabitat Structure

Results showed little evidence of a relationship between morphology and microhabitat when conventional statistical analyses were used, and no evidence when phylogenetically controlled statistical analyses (PANOVA and PMANOVA) were used, coinciding with previous studies (Jaksić et al., 1980; Schulte et al., 2004; Pincheira-Donoso et al., 2009). An alternative analysis, the phylomorphospace, whilst it did show instances of vast differences between some closely related species based on microhabitat and some incidences of convergent evolution, there was no clustering present based on microhabitat, explaining the lack of significant results.

Due to the intrinsic link between morphology and locomotor performance as a result of the differing physical demands in different habitats (Moermond, 1979; Pounds, 1988; Herrel et al., 2002) and body shape itself varying considerably among species with similar

body sizes, it would be expected that morphology evolves to provide optimal performance in the habitat occupied. Previous studies have found a relationship between morphology, performance ability and openness of microhabitat (Melville & Swain, 2000; Losos, 2009). Open ground *Liolaemus* species were generally found to have a comparatively wide body based on their position in morphospace, as is the case in open ground species in previous studies (Pounds, 1988; Melville & Swain, 2000; Collar et al., 2011). However, this was not supported by statistical analysis, as open ground species were not significantly different from other microhabitat groups in phylogenetically controlled analysis and only open-ground shrub species in traditional analysis. These findings do not correspond to the hypothesis that open ground species would be intermediate in width. Ground-dense vegetation species do not tend to have a particularly slender body based on their position in morphospace, as is the case in previous studies (Pounds, 1988; Melville & Swain, 2000; Collar et al., 2011), and statistical analysis does not show any significant difference from any other microhabitat categories. Open ground-shrub species are very diverse, occupying the vast majority of morphospace. This is potentially due to terrestrial species being less constrained; previous studies suggest arboreal and rock-dwelling species are constrained size-wise due to the need for clinging and the ability to hide in crevices (Deban et al., 1994), whilst terrestrial species do not have these constraints (Collar et al., 2011). Moreover, there are more ecological opportunities for species to utilize certain habitats, such as ground habitats, compared to others, such as twig habitats (Collar et al., 2010). These two factors may have allowed the open ground-shrub microhabitat group to evolve such diverse body shape and explain why this group did not follow the hypothesis that open-ground shrub species would have an intermediate body shape with a slight tendency to being narrower and why significant differences were not found.

Vast differences are present between different types of arboreal species, i.e. trunk and branch species (comparable to the twig species in this study), and are also dependant on the size of the tree (Kohlsdorf et al., 2001; Collar et al., 2011). Twig species in this study are located in the region of morphospace that exhibit narrow bodies, as found previously in many other genera, as narrow bodies assist in balancing on a narrow perch, preventing toppling (Pounds, 1988; Losos, 1990b; Melville & Swain, 2000; Martins et al., 2001; Losos, 2009; Collar et al., 2011). Tree trunk species were broader than twig species and many other species based on their location in morphospace. However, statistical analysis did not support these finding, thus the hypothesis that twig species and tree trunk species would represent the extremes of body width is not supported.

The challenges faced by species that use climbing for locomotion is dependent on substrate. Twig species' main challenge is not toppling sideways (Losos & Sinervo, 1989), whereas, saxicolous species' main challenge is to not topple backwards (Zaaf & Van Damme, 2001). Thus saxicolous species tend to have a compressed, wide and flat, body shape (Deban et al. 1994; Vitt et al. 1997; Melville & Swain 2000; Goodman 2007; Revell et al. 2007; Goodman & Isaac 2008; Collar et al. 2011). This is somewhat the case in *Liolaemus*; male saxicolous species are relatively wide, female saxicolous species less so. The wideness of the male saxicolous species would appear to support the hypothesis that saxicolous species have wide bodies, however, they were not significantly separated from other microhabitat categories, thus the hypothesis is not supported by statistical analysis. The degree of flatness is one of the main adaptations of saxicolous species, and is key in differentiating them from terrestrial species (Aerts et al., 2000). Using only two dimensions would have missed this difference; three-dimensional analysis of shape would potentially show evidence of ecomorphs.

5.1.1 Sexual Dimorphism

Males and females were significantly separated in morphospace. These differences were expected as both sexes are known to experience the same natural selection pressures in different ways, given their differing reproductive and parental roles. Females are generally under fecundity selection, whereas males select for optimized performance to defend territory (Braña, 1996; Herrel et al., 2002; Cox et al., 2003; Huyghe et al., 2005; Lappin & Husak, 2005). The location in morphospace of the females in regards to males in the same microhabitat showed that females have a narrower, shorter trunk, a narrower but longer neck and an elongated snout. This is not what would be expected if selection on females was due to fecundity, as a trunk with a larger volume would be expected to hold more eggs (Du et al., 2005; Du & Lü, 2010) and is a trait that is often found in females (e.g. Olsson et al. 2002; Pincheira-Donoso & Tregenza 2011). However, based on findings by Goodman et al. (2009) reduced abdominal volume may not in fact reduce reproductive output, as females become "fuller" of eggs when their abdominal volume is reduced. Thus, different factors may be acting on females (see parity section for further discussion). Overall, this matches the hypothesis that males and females will differ in morphology, but not as expected, with females being wider.

The increased significant separation between microhabitat groups in males (open ground-shrub and tree trunk microhabitat groups) when compared to females (no significant separation between any groups) may be due to males being under a strong selective pressure to have optimal locomotor performance. This is exemplified in lizards where territoriality is correlated strongly with locomotor performance (Garland et al. 1990; Robson & Miles 2000) and males having stronger adaptive responses than females (Herrel et al., 2002). As territoriality has been found to be a driver for habitat specialization (Losos et al., 1998; Irschick & Losos, 1999), territorial males would be expected to be more likely to show evidence of ecomorphs, therefore it is possible only territorial males would show clear ecomorphotypes.

As head and body were analysed separately for the purpose of investigating the effects of parity, it allowed further investigation of the differences between the sexes. Instances of dimorphism in shape between the sexes generally occur within the head (heads tend to be larger in males; Boretto et al., 2007; Olsson et al., 2002; Teixeira-Filho et al., 2003) and trunk (larger in females, Braña 1996; Cox et al. 2003). Contradictory to this, very little variation in head shape was found. However, this is likely due to landmarks being selected to describe shape rather than to relate to specific functions, such as landmarks placed based on musculature (Stayton, 2006). Conversely, looking at only the body, males and females occupied different regions of morphospace, thus it seems likely that females are under different selection pressures to males.

5.1.2 Why may evidence of ecomorphs not have been found?

Evidence of a relationship between limb length and tails, and habitat use is present in many lizards (Pianka & Pianka 1976; Pounds 1988; Losos 1990b; Losos 1990a; Vitt et al. 1997; Irschick & Losos 1999; Melville & Swain 2000; Vanhooydonck et al. 2000; Bickel & Losos 2002; Herrel et al. 2002; Goodman 2007; Goodman et al. 2008; Losos 2009; Grizante et al. 2010; Collar et al. 2011). Here the omission of limb and tail shape may have prevented the identification of ecomorphs. As the tail is used for balance, it would be expected to be longer in rock and arboreal species whilst being shorter in ground species, which minimises weight thereby increasing efficiency (Collar et al., 2011; Martins et al., 2001). In spite of this there is a lack of evidence of tail length varying by habitat type in anoles (Pounds 1988) and *Liolaemus* (Jaksić et al., 1980; Schulte et al., 2004; Pincheira-Donoso et al., 2009), potentially as length is not the best measure of size

for a counterbalance (Pounds 1988). Morphometrics would be able to examine if there is any differences in tail shapes between microhabitat groups. Whilst previous studies have taken extensive measurements of *Liolaemus* limbs (Schulte et al., 2004; Pincheira-Donoso et al., 2009), no efforts have been made to quantify limb shape, which may be an important factor, specifically in terms of locomotion.

A further potential factor is the omission of locomotory information in this study. As morphology is closely linked to locomotion (Pounds, 1988; Losos, 1990b, 1990a), species that occupy the same microhabitat but use it differently may develop different body shape. For example, different relationships were found within different rock habitats (Vitt et al., 1997; Melville & Swain, 2000; Vanhooydonck et al., 2000; Herrel et al., 2002; Goodman, 2007; Goodman & Isaac, 2008; Goodman et al., 2008) either due to differences between the rock habitats requiring differing locomotory means or using different behaviours. The structure of the habitat is considered important in determining locomotion; a habitat where another appropriate microhabitat structure is in close proximity leaping is an effective means of moving, whereas on isolated or sparse branches and trunks, running and crawling is more efficient (Losos, 1990b, 1990a). There is also a relationship between sprint speed and type of habitat (Melville & Swain, 2000). *Anolis* species become slower as the surface becomes narrower. For some species the decrease in speed is greater than in others, (i.e. sprint sensitivity) thus species that experience substantial declines in speed would avoid narrower surfaces (Irschick & Losos, 1999; Losos & Sinervo, 1989). It may be the case that for *Liolaemus* that the relationship between surface diameter and speed does not hold true. There is evidence of differing morphologies resulting in similar patterns of locomotor evolution due to different kinematic strategies; for example, axial bending and longer hindlimbs both result in longer stride length (Bergmann & Irschick, 2010). Differences in posture could also prevent the evolution of a relationship between morphology and performance (e.g. a species with a sprawling posture can compensate for shorter limbs by moving them under the body, thereby giving them a functionally longer limb length, Vanhooydonck et al., 2000).

Moreover, the categorization of species may not be sufficient as too broad a categorization can prevent the identification of ecomorphs (Blankers et al., 2013) as specializations can only be identified for specific substrates with differing locomotory mechanisms (Kohlsdorf et al., 2001). Several of the categories potentially utilised similar locomotory means such as open ground-shrubs and ground-dense vegetation. This could potentially be overcome by using the percentage of different substrates used rather than

definitive groups (Grizante et al., 2010). *Liolaemus* habitats tend to be broad, flat and usually horizontal and as such may not vary enough to evolve differing body shape (Schulte et al., 2004). Open ground and open ground shrub on the other hand were significantly separated, suggesting that although the habitat types were similar, different locomotory means could have evolved. Further to this, substrate slope has not been investigated (Kohlsdorf et al., 2001). A relationship between substrate and clinging ability in *Liolaemus* has been found. Species that encounter vertical surfaces regularly have differences in pad area, claw height and toe length thus present significantly better clinging abilities, arboreal more so than saxicolous (Zani, 2000; Tulli et al., 2011). This shows substrate slope has an effect on at least some aspects of morphology. Thus, it may be that species have evolved specific adaptations to their microhabitats, but not in the traits investigated in this study. It has also been suggested that these key adaptations are more important than other aspects, such as limb size, and thus effectively removes constrictions placed by the environment (Zaaf & Van Damme, 2001; Goodman & Isaac, 2008; Losos, 2009; Tulli et al., 2011).

Alternatively, ecomorphs might be being prevented from evolving due to several factors, including a lack of coevolution (Vanhooydonck et al., 2000; Losos et al., 2003) Furthermore, selection within species using the same habitat could be weaker if time in that habitat to evolve optimum morphology has been shorter (Collar et al., 2011). Moreover, much evidence of shared morphology and environments is found on islands (e.g. Arnegard et al., 1999; Gillespie 2004). While there is some evidence of convergence on mainland, even on differing continents (Melville et al., 2006) and a recent study has found that similar patterns of adaptive radiations can occur on both islands and continents (Pincheira-Donoso et al., 2015), it could be that there are too many differing ecological factors effecting the evolution of morphology in mainland species such as *Liolaemus* for them to evolve similar body plans, such as greater numbers of predators, more competitors and larger climatic ranges (Vidal et al., 2006; Losos, 2009; Yoder et al., 2010; Blankers et al., 2013). This is further supported by a study that found island specimens of *L. pictus* were substantially different to mainland specimens as a result of differing pressures resulting in differing diets (Vidal et al., 2006). As such, it could be that other factors are determining the vastly differing body plans in *Liolaemus* which will be discussed in the following section.

5.2 Additional Potential Factors Affecting the Evolution of Body Shape

5.2.1 Diet

Diet has been found to be a fundamental factor in determining morphology, physiology, ecology and behaviour (Valdecantos et al., 2012). Herbivorous *Liolaemus* are significantly different from insectivorous ones, whilst omnivorous species are significantly different from neither herbivorous nor insectivorous. This is expected as vastly different morphological, physiological and behavioural features are needed for herbivorous and insectivorous (or carnivorous) species (Zimmerman & Tracy, 1989; Espinoza et al., 2004; Stayton, 2006; Valdecantos et al., 2012). The location of omnivorous species within morphospace is centrally, thus have neither a particularly wide or narrow trunk, nor a particularly large or small head, but rather intermediate. Given *Liolaemus* has evolved gradually to herbivores from omnivores, not directly from insectivores (Espinoza et al., 2004) the similarity is to be expected. However, these results indicate no significant difference between different groups when phylogeny is taken into account. It may be that the species are similar due to relatedness, not diet, and that diet type has simply evolved nearby on the tree. Alternatively, it was an adequate adaptation already present in a common ancestor and has been retained (Losos, 1990b). It could also be due to species sampling; herbivory has evolved repeatedly in *Liolaemus*, with multiple origins (Espinoza et al., 2004), whereas the herbivorous species included in this study were all closely related.

Herbivorous lizards are generally large as a warm body temperature is needed to digest plant material (Pough, 1973). Interestingly however, *Liolaemus* herbivores tend to be small due to the cold climate they occupy (Espinoza et al., 2004). However, *Liolaemus* exhibit a low PC2 score and are as such somewhat wider potentially to provide a larger surface area to absorb heat and to accommodate a larger gut required for the digestion of plant matter (Zimmerman & Tracy, 1989). Herbivorous species in this study are consistent with the hypothesis of having a wider, longer snout, which is somewhat expected due to the increased bite force, which is needed for cropping plants (Herrel et al., 1998, 2008), and is associated with a wide head (Lappin & Husak, 2005). These findings also correspond to previous findings where they found that male herbivorous *Liolaemus* had long heads and short snouts, which are consistent with high bite force; whereas females were found to have short, narrow heads, compensating for expected reduced bite force with long snouts, and thus more space for muscles (Vanhooydonck et al., 2010).

There is also a behavioural link between diet, or rather foraging mode, and morphology. For example, morphological variation between arboreal sit and wait, that tend to be wide-bodied, and widely foraging, that tend to be slender-bodied, ground dwelling species has been found repeatedly (Scheibe 1987; Losos 1990a; Losos et al. 1998; Vanhooydonck et al. 2006; Collar et al. 2011). The large variation in snout size, both width and length, in insectivorous species could be due to different types of prey consumed (Herrel et al., 2008; Valdecantos et al., 2012). Variations within the same dietary group could also be explained by differing shape changes leading to the same resulting function, such as different adaptations causing similar increases in mechanical advantage (Stayton, 2006). Subsequently, species adapted for the same function are located in different regions of morphospace. Therefore, investigating function, which this study did not include, in relation to diet in *Liolaemus* could provide an insight into the evolution of morphology.

Herbivorous species also have an increased time of digestion and absorption and as such a food takes longer to travel through the gut (Zimmerman & Tracy, 1989). Due to this herbivorous species would have increased burden and as such may need alternative adaptations to compensate for escaping reactions. A trade-off has been found between bite-force and climbing speed. Shorter heads result in faster climbing speeds as taller heads move the centre of mass away from the substrate, effectively pulling the lizard away from the substrate and causing the animal to topple backwards (Vanhooydonck et al., 2007). However, shorter heads generate lower bite force, as the muscles are in a less favourable position to generate high forces (Herrel et al., 2001). Therefore, it may be expected that diets requiring high bite force might preclude adaptations that would have otherwise evolved for species living in microhabitats requiring climbing.

5.2.2 Parity Mode

As abdomen volume is important for reproductive output, body size and relative abdomen length have been found to be higher in females than in males (Medina & Ibargüengoytía, 2010; Yang et al., 2012). While this is not always the case (Goodman et al., 2009), larger *Liolaemus* females have been found to result in higher fecundity (Pincheira-Donoso & Tregenza, 2011). In this study, none of the viviparous species are as slender as the most slender oviparous species and viviparous species require a larger abdominal volume to produce the same number of offspring. However, viviparous species are not consistently as broad as there is potential for. This could be due to environmental constraints (Climate:

Schulte et al., 2000; Pincheira-Donoso et al., 2013; food resources: Shine, 2005; degree of specialization: Pianka & Pianka, 1976), or as a direct result of the colder climates viviparous species occupy (Pincheira-Donoso et al., 2013), i.e. colder climates promote the evolution of higher rates of accumulation of body fat (Boretto et al., 2007). On the other hand, there is also evidence that some lizards do not compensate for reduced output by modifying maternal body size or shape (Yang et al., 2012). Species that are 'fuller' than others to compensate for their reduced body volume suggest that species are full to a level that is optimal not what they are maximally capable (Du et al., 2005; Goodman et al., 2009; Du & Lü, 2010). Therefore, it is clear that more factors are relevant to reproductive output than abdominal size, and thus it is not surprising that there is variation in shape between but also within parity modes and that morphology does not necessarily reflect what is initially expected and that the hypotheses are not met.

Blackburn (2000) and Shine (2006) stated the importance of confirming a functional link between the point at which the perceived adaptation evolved and this coinciding with, or occurring after, the evolution of viviparity, rather than being a preadaptation. As such it could be argued that this study potentially indicates that the adaptations perceived to be related to viviparity are preadaptations, as there were no significant differences between viviparous and oviparous species when phylogeny was taken into account. However, evidence has been found to show that evolution of functional adaptations needed for viviparity coincide with transitions to viviparity in *Liolaemus* (Pincheira-Donoso et al., 2013). Furthermore, viviparity has evolved multiple times in *Liolaemus* (Schulte et al., 2000), Thus, this explanation seems unlikely and may be better explained by the species included in this analysis.

5.2.3 Behaviour

As behaviour coevolves with morphology (Losos, 1990b, 1990a) behaviour needs to be taken into consideration when looking at morphological adaptations. Whilst there are many behaviours that could alter morphological evolution such as thermoregulation (Huey et al., 2003), locomotion (see above), and foraging behaviour (see above, but see also: Shine 2005; Boretto, Jorgelina et al., 2007), here the focus will be on escape behaviour, as this is a fundamental behaviour to survival and fitness.

If species escape into a microhabitat that differs to the one in which they spend most of their time, these species may be better adapted to the habitat they escape to (Pounds,

1988), as seen in the morphology of *L. lemniscatus*, which fled from rocks or ground to grassy patches, and *L. fuscus*, which remained on rocks when fleeing from a predator (Jaksić & Núñez, 1979). They also determined that the colouration of the species acted as camouflage in microhabitats they escaped to, thus it would be interesting to investigate the colouration of species and determine if this correlates to their predominate habitat and, if not, if it can be used to determine what habitat species escape to and if their morphological adaptations are suited to this rather than to their predominant microhabitat. Furthermore, as evidence has been found that maximal sprinting ability is used only when escaping from predators in Anolis (Irschick & Losos, 1998), predation pressures may have an effect on morphological adaptations. Predation pressure could be investigated through the number of lizards with broken tails in varying locations (Pianka & Parker, 1972; Pianka & Pianka, 1976) as a proxy for predation, however success rates of predators may vary. Thus it would be important to look at type of predators and their behaviour, such as the use of persistence rather than speed, adaptation for endurance, rather than speed, would be more important (Pounds, 1988). As there is a functional trade-off between speed and endurance (Vanhooydonck et al., 2007), if some *Liolaemus* are more adapted for endurance then it would affect the morphological outcome of these species as they would have different morphological adaptations to cope with the differing strategies. Furthermore, different predator types have resulted in two different escape methods in saxicolous species, resulting in different morphologies (Goodman, 2007; Revell et al., 2007).

Another factor to be considered is that species and individuals that have compromised sprinting ability tend to use alternate escape behaviour, such as crypsis (Irschick & Losos, 1998). Whilst there is evidence of a link between microhabitat type and escape behaviour, such as dense vegetation and increased used of crypsis, or open habitats and sprinting for escape (Losos & Irschick, 1996; Irschick & Losos, 1998; Irschick & Losos, 1999; Melville & Swain, 2000), Schulte et al. (2004) found contrasting evidence for escape behaviour in *Liolaemus*, suggesting that crypsis is used in open spaces by *Liolaemus*. Thus adaptations for crypsis may outweigh adaptations to moving at optimum effectiveness in the microhabitat. Furthermore, in lizards where patterns of convergent evolution have been found exceptions are due to differences in escape behaviour such as escaping down nearby spider burrows in open ground (Pianka & Pianka, 1976). Different escape means in the same microhabitat (e.g. Pounds, 1988) would lead to different

morphological adaptations. Thus analysis of microhabitat categories and escape means as a cofactor could be used to see if this explains morphological differences.

5.2.4 Temperature

Temperature has also been found to be a fundamental factor in determining morphology. For example, in contrast to findings that suggest that densely vegetated habitats result in slender lizards (Pounds, 1988; Melville & Swain, 2000; Losos, 2009; Collar et al., 2011) temperate zone lizards were found to be bulky in these environments, and slender in more open habitats (Scheibe, 1987). However, this was when climate was included as a factor; the bulky lizards found in densely vegetated locations were also associated with a cooler climate, whereas the slender lizards in the open environments were also warmer. As such if temperature were taken into account, *Liolaemus* may exhibit ecomorphotypes within a specific temporal range.

There are many other factors that could also be determining morphology that have not been discussed here, including sexual selection, ecosystem rainfall, humidity, elevation, environment, complexity of environment and range size (see: Pincheira-Donoso et al., 2009).

5.3 Phylogenetic Patterns of Body Shape Evolution

The results obtained here of a low phylogenetic signal (K <1) for morphology coincide with previous values obtained for phylogenetic signal within *Liolaemus* when looking at morphology and size (Tulli et al., 2011), indicating a departure from BM. λ values also indicate departure from BM. This suggests that closely related species do not have similar body shapes and are, as expected based on the hypothesis of low phylogenetic signal as a result of evolution, being pushed in a specific direction. Furthermore, it suggests *Liolaemus* morphology is evolutionary labile (Tulli et al., 2011; Cruz et al., 2011). This could be due to either distantly related species resembling each other more than expected, such as seen in convergent evolution, or that closely related species resemble each other less than expected, as seen in character displacement (Blomberg et al., 2003). λ values were also significantly different from 0, suggesting that species are not independent and some morphological evolution is as a result of shared history. Contradictory to the results of Tulli et al., (2011), K for SVL was not significantly different from 1, suggesting the presence of phylogenetic signal for SVL, but does correspond to the findings of Vanhooydonck et al. (2010). However, Tulli et al. (2011) highlighted the effect of species sampling and features considered on phylogenetic signal within *Liolaemus*, as such the species used in this study may have had a substantial effect on the K-statistic obtained.

The hypothesis of morphological evolution following an OU model of evolution was upheld in this study for SVL and PC1-3. OU coincides with the low K value as distantly related species would resemble each other more than expected in this model (Blomberg et al., 2003). This finding also corresponds to previous findings of the evolution of body size in *Liolaemus* (Pincheira-Donoso et al., 2015). An OU model with 3 optima being the best fit for SVL suggests that body size may be related to diet, whereas for PC1-3 an OU model with 6 optima was the best fit, suggesting potential for morphological shape evolution to be driven by microhabitat.

Body size and body shape evolution both matched the hypothesis when fitting the δ model; slow initial evolution, followed by rapid evolution in recent history, this also corresponds to previous findings of evolution of *Liolaemus* body size (Pincheira-Donoso et al., 2015). Results for κ, on the other hand, did not match the prediction that evolution would be proportionately higher in in long branches, for SVL, PC1 and PC2, evolution was proportionately lower in longer branches. For PC3 evolution was punctuational. This fits with the lack of evidence for ecomorphs as the hypothesised pattern of evolution for

κ would be expected if ecomorphs were present (Thomas et al., 2009; Thomas & Freckleton, 2012).

PC1 and SVL showed a significant relationship, therefore on PC1 size can be somewhat predicted by shape, as has been found to be the case in other lizards (e.g. Collar et al., 2011) and suggests a region of morphospace is specific to a particular size of lizard (Stayton, 2006). This was not the case for PC2 and PC3. The best fitting model for PC1 and PC2 included microhabitat and diet as factors, but not parity, this suggests that parity does not significantly contribute to the model, therefore the predicting of shape does not appear to be influenced by parity more. Conversely, the best model to describe PC3 includes diet and parity, but not microhabitat, thus parity does contribute to the prediction of shape on the third PC axis, whereas microhabitat does not. However, parity modes are not significantly separated on any axis. For PC1, insectivorous and herbivorous are significantly separated, suggesting that shape may be predictable for these dietary groups. For PC2 pairwise comparisons showed that microhabitat groups were not significantly different when controlling for SVL aside from for PC2 open ground and open ground-shrub species, therefore it seems reasonable to suggest shape cannot be a predictor for microhabitat.

The hypothesis of increased evolutionary rates is met in PC1, though cannot be matched to specific drivers, it is not met in PC2 or PC3. The lineages that have been identified as experiencing increased evolutionary shift on PC1 constitute three of the rock species present in this study. PC1 explains substantial variation in the size of the trunk, both width and length. Rock-dwelling species are adapted to be wide and flat (Deban et al., 1994; Vitt et al., 1997; Melville & Swain, 2000; Goodman, 2007; Revell et al., 2007; Goodman & Isaac, 2008; Collar et al., 2011) thus, the majority of change would occur in these species on the first PC axis and may have caused them to evolve rapidly to adapt the morphology required for living on rocks. This is yet another way in which *Liolaemus* have been found to be different to other lizards as Collar et al. (2010) found slower rates of evolution in rock-dwelling dragon lizards when compared to terrestrial and semi-arboreal. It was suggested that this was due to the limited ways to make use of a rocky habitat (Collar et al., 2010) however, dependant on several factors including: the smoothness of rocks, the density of vegetation, the proximity of the rocks, and differences in behaviour, morphology can vary vastly (Vitt et al., 1997; Melville & Swain, 2000; Vanhooydonck et al., 2000; Herrel et al., 2002; Goodman, 2007; Goodman & Isaac, 2008; Goodman et al., 2008). Furthermore, the species that experienced an increased

evolutionary rate are omnivorous and viviparous, both of which require a specific set of adaptations thus may have needed to evolve rapidly to evolve these traits. This is somewhat contradictory to the decreased evolutionary rate on PC2 as these species include four different microhabitat types and thus would be expected to evolve more rapidly to reach the required morphological adaptations for the vastly different physical demands. However, this could explain why ecomorphological separation has not been reached. The decreased rate of evolution on PC3 may be due to the lack of diversification within these species, all four are open-ground shrub species, three of which are insectivorous and oviparous, only one species, *L. irregularis*, is omnivorous and viviparous.

5.4 Conclusions

The *Liolaemus* lizard radiation has attained exceptional diversity and occupation of extensive habitats through divergent and convergent evolution. However, this study corroborates previous findings involving the lack of signals of replicated processes of adaptation in response to exposure to similar natural selection regimes. *Liolaemus* appear to lack a relationship between morphology and structural microhabitat. Potential explanations for the lack of ecomorphological relationships are that either other ecological factors exert a stronger pressure on the evolution of morphology and as such they have not evolved, or ecomorphological adaptations are present but methodologies are not appropriate to identify them. To determine if *Liolaemus* are microhabitat specialists, behaviour would need to be considered. Furthermore, as several observed adaptations between different microhabitats is the degree of dorso-ventral flattening, three-dimensional analyses may unveil previously unobserved relationships.

6 References

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7 Tables and Figures

Table 1: List of species, number of specimens and microhabitat occupied.

Species	Total	Female	Male	Microhabitat	Diet	Parity Mode
Liolaemus andinus/molinai	39	20	19	Open ground	Omnivorous	Viviparous
Liolaemus archeforus	29	12	17	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus baguali	16	5	11	Open ground-shrubs	Insectivorous	Viviparous
Liolaemus bellii	33	15	18	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus bibronii	18	3	15	Ground-dense vegetation	Insectivorous	Oviparous
Liolaemus boulengeri	26	17	9	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus buergeri	14	8	6	Rocks	Omnivorous	Viviparous
Liolaemus canqueli	19	6	13	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus ceii	8	4	4	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus chacabucoense	12	6	6	Open ground-shrubs	N/A	N/A
Liolaemus chehuachekenk	12	3	9	Ground-dense vegetation	Omnivorous	N/A
Liolaemus chiliensis	5	2	3	Twigs	Insectivorous	Oviparous
Liolaemus coeruleus	26	12	14	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus constanzae	43	13	30	Open ground-shrubs	Omnivorous	Oviparous
Liolaemus curicensis	34	19	15	Ground-dense vegetation	Insectivorous	Viviparous
Liolaemus curis	22	10	12	Rocks	Insectivorous	Viviparous
Liolaemus darwinni	9	4	5	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus elongatus	13	6	7	Rocks	Omnivorous	Viviparous
Liolaemus escarchadosi	23	9	14	Rocks	Insectivorous	Viviparous
Liolaemus fitzingerii	29	10	19	Open ground-shrubs	Omnivorous	Oviparous
Liolaemus gallardoi	8	2	6	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus goetschi	5	3	2	Open ground-shrubs	Omnivorous	Oviparous
Liolaemus gracilis	5	2	3	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus grosseorum	6	5	1	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus irregularis	21	11	10	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus kingii	22	8	14	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus kolengh	31	15	16	Ground-dense vegetation	Insectivorous	Viviparous
Liolaemus koslowskyi	6	4	2	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus kriegi	17	9	8	Open ground-shrubs	Omnivorous	Viviparous

Liolaemus lemniscatus	43	22	21	Ground-dense vegetation	Insectivorous	Oviparous
Liolaemus leopardinus	17	11	6	Rocks	Omnivorous	Viviparous
Liolaemus lineomaculatus	32	16	16	Open ground-shrubs	Herbivorous	Viviparous
Liolaemus magellanicus	12	8	4	Ground-dense vegetation	Omnivorous	Viviparous
Liolaemus manueli	12	5	7	Open ground	Insectivorous	Viviparous
Liolaemus melanops	17	2	15	Open ground-shrubs	Omnivorous	Oviparous
Liolaemus morenoi	3	0	3	Open ground-shrubs	Omnivorous	Oviparous
Liolaemus nigriceps	4	3	1	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus nigroviridus	45	20	25	Rocks	Omnivorous	Viviparous
Liolaemus nitidus	24	15	9	Rocks	Omnivorous	Oviparous
Liolaemus paulinae	17	8	9	Open ground-shrubs	Insectivorous	Viviparous
Liolaemus periglacialis/hatcheri	21	8	13	Open ground-shrubs	Herbivorous	Viviparous
Liolaemus petrophilus	10	4	6	Rocks	Omnivorous	Viviparous
Liolaemus pictus	17	5	12	Tree trunks	Omnivorous	Viviparous
Liolaemus pseudoanomalus	3	0	3	Open ground	Insectivorous	Oviparous
Liolaemus rothi	14	7	7	Open ground-shrubs	Omnivorous	Oviparous
Liolaemus sarmientoi	5	4	1	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus scolaroi	21	9	12	Open ground-shrubs	Insectivorous	Viviparous
Liolaemus scroochi	5	0	5	Rocks	Omnivorous	Viviparous
Liolaemus shehuen	1	0	1	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus silvanae	37	17	20	Open ground-shrubs	Herbivorous	Viviparous
Liolaemus somuncurae	23	11	12	Open ground-shrubs	Omnivorous	Viviparous
Liolaemus tari	18	13	5	Ground-dense vegetation	Insectivorous	Viviparous
Liolaemus telsen	15	4	11	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus tenuis	34	19	15	Tree trunks	Insectivorous	Oviparous
Liolaemus torressi	5	3	2	Open ground	Insectivorous	Viviparous
Liolaemus tregenzai	8	5	3	Open ground-shrubs	Herbivorous	N/A
Liolaemus tristis	18	10	8	Open ground-shrubs	Insectivorous	Viviparous
Liolaemus uptoni	6	1	5	Open ground-shrubs	Insectivorous	Viviparous
Liolaemus wiegmanii	8	6	2	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus xanthoviridis	24	7	17	Open ground-shrubs	Insectivorous	Oviparous
Liolaemus zapallarensis	37	19	18	Open ground-shrubs	Omnivorous	Oviparous
Liolaemus zullyi	14	5	9	Open ground-shrubs	Insectivorous	Viviparous

Table 2: Location of landmarks.

Landmark	Location
1	The most anterior point of the snout
2	The most anterior point of the ocular semicircle on the left
3	The most anterior point of the ocular semicircle on the right
4	The widest point of the ocular semicircle on the left
5	The widest point of the ocular semicircle on the right
6	The most posterior point of the ocular semicircle on the left
7	The most posterior point of the ocular semicircle on the right
8	The pineal eye
9	The cheek, behind the pineal eye, on the left
10	The cheek, behind the pineal eye, on the right
11	Behind the ear on the left
12	Behind the ear on the right
13	The point at which the neck is narrowest on the left
14	The point at which the neck is narrowest on the right
15	The anterior most point of where the forelimb join the body on the left
16	The anterior most point of where the forelimb join the body on the right
17	The posterior most point of where the forelimb join the body on the left
18	The posterior most point of where the forelimb join the body on the right
19	On the left side of the body approximately equidistant on the curve from the forelimb and landmark 21
20	On the right side of the body approximately equidistant on the curve from the forelimb and landmark 22
21	On the left side of the body approximately equidistant on the curve from landmark 19 and the hind limb
22	On the right side of the body approximately equidistant on the curve from landmark 20 and the hind limb
23	The anterior most points of where the hind limb join the body on the left
24	The anterior most points of where the hind limb join the body on the right
25	The posterior most points of where the hind limb join the body on the left
26	The posterior most points of where the hind limb join the body on the right

Table 3: Amount of variance explained in each principal component axis based on eigenshape analysis.

PC axis	Eigenvalues	% Variance	Cumulative %
1	0.000697	33.103	33.103
2	0.000531	25.243	58.346
3	0.00022	10.437	68.782
4	0.000113	5.363	74.145
5	8.24E-05	3.916	78.061
6	6.09E-05	2.893	80.954
7	5.75E-05	2.733	83.687
8	5.19E-05	2.464	86.151
9	4.67E-05	2.219	88.37
10	4.11E-05	1.951	90.321
11	3.47E-05	1.647	91.968
12	2.87E-05	1.364	93.332
13	2.42E-05	1.15	94.482
14	2.19E-05	1.041	95.524
15	1.8E-05	0.857	96.38
16	1.45E-05	0.687	97.068
17	1.21E-05	0.576	97.644
18	1.14E-05	0.542	98.186
19	1.01E-05	0.48	98.666
20	8.17E-06	0.388	99.054
21	7.1E-06	0.337	99.391
22	6.52E-06	0.31	99.701
23	4.47E-06	0.213	99.913
24	1.82E-06	0.087	100

Table 4: Amount of variance explained in each principal component axis based on eigenshape analysis for the head.

PC axis	Eigenvalues	% Variance	Cumulative %
1	0.00152877	25.929	25.929
2	0.00146284	24.81	50.739
3	0.0010677	18.109	68.847
4	0.00067472	11.443	80.291
5	0.00032375	5.491	85.782
6	0.00025612	4.344	90.126
7	0.00020965	3.556	93.681
8	0.00019459	3.3	96.982
9	0.00012437	2.109	99.091
10	0.00005359	0.909	100

Table 5: Amount of variance explained in each principal component axis based on eigenshape analysis for the body.

PC axis	Eigenvalues	% Variance	Cumulative %
1	0.001261	41.876	41.876
2	0.000498	16.554	58.429
3	0.000448	14.873	73.302
4	0.000201	6.672	79.974
5	0.000134	4.467	84.441
6	0.000128	4.251	88.692
7	9.67E-05	3.212	91.904
8	6.76E-05	2.244	94.148
9	6.43E-05	2.136	96.284
10	4.61E-05	1.529	97.813
11	3.55E-05	1.178	98.991
12	3.04E-05	1.009	100

Table 6: Results for PANOVA, using only axis 1, and PMANOVA, using axes 1-2 and axes 1-3. Each analysis was carried out on the entire specimen on species, male and female averages for microhabitat, diet and parity. For parity, analysis based on only the head and only the body are also included.

Sex	Factor	PC Axes	Output
Species	Microhabitat	1	$F_{5,45}$=3.065, P=0.134
		1-2	$F_{10,88}$=2.792, P=0.082
		1-3	$F_{15,119}$=2.535, P=0.079
Male		1	$F_{5,45}$=2.286, P=0.236
		1-2	$F_{10,88}$=2.437, P=0.151
		1-3	$F_{15,119}$=2.011, P=0.230
Female		1	$F_{5,43}$=2.933, P=0.126
		1-2	$F_{10,84}$=1.884, P=0.316
		1-3	$F_{15,114}$=2.039, P=0.191
Species	Diet	1	$F_{2,96}$=2.494, p=0.213
		1-2	$F_{4,94}$=1.991, P=0.340
		1-3	$F_{6,92}$=1.360, P=0.569
Male		1	$F_{2,96}$=3.904, P=0.096
		1-2	$F_{4,94}$=2.553, P=0.205
		1-3	$F_{6,92}$=1.800, P=0.375
Female		1	$F_{2,92}$=1.668, P=0.356
		1-2	$F_{4,90}$=2.691, P=0.162
		1-3	$F_{6,88}$=1.808, P=0.379
Species	Parity	1	$F_{1,48}$=2.948, P=0.490
		1-2	$F_{2,47}$=4.016, P=0.528
		1-3	$F_{3,46}$=2.910, P=0.705
Male		1	$F_{1,48}$=1.503, P=0.640
		1-2	$F_{2,47}$=3.673, P=0.563
		1-3	$F_{3,46}$=2.503, P=0.757
Female		1	$F_{1,46}$=2.975, P=0.468
		1-2	$F_{2,45}$=4.3195, P=0.443
		1-3	$F_{3,44}$=3.257, P=0.641
Species	Parity (Head Only)	1	$F_{1,48}$=0.890, P=0.704
		1-2	$F_{2,47}$=0.510, P=0.915
		1-3	$F_{3,46}$=3.203, P=0.664
		1-4	$F_{4,45}$=4.016, P=0.629
Male		1	$F_{1,48}$=1.167, P=0.645
		1-2	$F_{2,47}$=0.575, P=0.897
		1-3	$F_{3,46}$=3.495, P=0.635
		1-4	$F_{4,45}$=5.185, P=0.501
Female		1	$F_{1,46}$=0.568, P=0.749
		1-2	$F_{2,45}$=1.063, P=0.839
		1-3	$F_{3,44}$=2.801, P=0.671
		1-4	$F_{4,43}$=2.349, P=0.817
Species	Parity (Body Only)	1	$F_{1,48}$=6.193, P=0.310
		1-2	$F_{2,47}$=3.647, P=0.558
		1-3	$F_{3,46}$=3.018, P=0.703
Male		1	$F_{1,48}$=6.826, P=0.296
		1-2	$F_{2,47}$=3.684, P=0.556
		1-3	$F_{3,46}$=2.815, P=0.697
Female		1	$F_{1,46}$=5.735, p=0.311
		1-2	$F_{2,45}$=3.870, P=0.512
		1-3	$F_{3,44}$=3.924, P=0.567

Table 7: Results for the fitContinuous test for lambda.

	log-likelihood	**AIC**	**Model Statistic**	**LR (p value) λ=0**	**LR (p value) λ=1**
SVL	18.9134	-31.83	λ=0.899	17.605 (0.00002718111)	45.610 (0.01652123)
PC1	*143.038*	*-280.08*	λ=0.466	14.197 (0.0001646693)	26.842 (0.0000002207597)
PC2	139.33	-272.66	λ=0.767	9.429 (0.002135939)	13.054 (0.0003026022)
PC3	*174.964*	*-343.93*	λ=0.544	7.539 (0.006036692)	33.049 (0.000000008986025)

Table 8: Results for the fitContinuous test of models of evolution

		log-likelihood	AIC	Model Statistic
SVL	**delta**	***19.437***	***-32.87***	δ=2.999
	OU	19.206	-32.41	α=0.102
	kappa	17.574	-29.15	κ=0.669
	BM	16.040	-28.08	
PC1	**OU**	**138.937**	**-271.87**	α=0.193
	delta	136.090	-266.18	δ=2.999
	kappa	135.455	-264.91	κ=0.299
	BM	129.617	-255.23	
PC2	**OU**	***139.676***	***-273.35***	α=0.172
	delta	138.211	-270.42	δ=2.999
	kappa	136.904	-267.81	κ=0.442
	BM	132.803	-261.61	
PC3	**kappa**	**172.626**	**-339.25**	κ=0.000
	OU	171.200	-336.4	α=2.399
	delta	165.515	-325.03	δ=2.999
	BM	158.440	-312.88	

Table 9: Results for OU model fit using the package OUCH to SVL and PC1-3, each with 1, 2, 3 and 6 optima.

	Number of Optima	Log-likelihood	AIC	Alpha (α) Value	Optima
SVL	1	19.068	-32.135	2.129	4.23052
	2	21.474	-32.949	2.737	4.08616 4.12528
	3	**31.789**	**-51.577**	**4.289**	4.00176 4.34136 4.05622
	6	26.535	-35.071	3.303	4.10185 4.11767 3.94183 4.38130 4.00910 4.55170
PC1	1	138.929	-271.858	3.757	-0.00417
	2	137.299	-264.598	7.322	-0.00891 -0.00520
	3	142.961	-273.923	8.558	-0.01193 -0.00467 0.01618
	6	**147.348**	**-276.696**	**16.056**	0.00453 -0.00379 0.00563 -0.01989 -0.03080 0.01336
PC2	1	139.659	-273.318	3.358	0.00208
	2	136.839	-263.678	3.798	0.00433 -0.00383
	3	139.982	-267.965	3.585	0.00317 -0.00002 0.01107
	6	**146.354**	**-274.709**	**3.508**	-0.03605 0.00246 0.00758 0.01500 0.00559 0.05075
PC3	1	171.200	-336.401	46.180	0.00657
	2	170.328	-330.655	10.770	0.00028 0.00005
	3	174.836	-337.672	8.438	0.00023 0.00210 -0.00552
	6	**177.927**	**-337.853**	**11.530**	0.00858 -0.00213 -0.00401 0.00417 0.00721 0.00167

Table 10: PGLS results for PC scores and SVL with and without microhabitat as a factor. The model compares microhabitat categories against the dense vegetation group.

	(PC axis~SVL)			**(PC axis~SVL+Microhabitat+Diet+Parity)**		
	PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
	t value (p value)	**t value (p value)**	**t value (p value)**	**t value (p value)**	**t value (p value)**	**t value (p value)**
Intercept	-3.063 (0.0035)	1.184 (0.2421)	0.366 (0.7159)	-2.591 (0.0133)	2.008 (0.0515)	1.196 (0.2387)
SVL	2.971 (0.0046)	-1.189 (0.2402)	-0.387 (0.7006)	2.968 (0.0051)	-2.764 (0.0086)	-1.070 (0.2910)
Microhabitat Ground-dense vegetation	-	-	-	0.218 (0.8290)	2.682 (0.0106)	-1.599 (0.1176)
Microhabitat Open-ground shrubs	-	-	-	-1.313 (0.1966)	3.598 (0.0009)	-1.635 (0.1099)
Microhabitat Rocks	-	-	-	-2.452 (0.0187)	4.097 (0.0002)	-0.671 (0.5064)
Microhabitat Tree trunk	-	-	-	-2.470 (0.0179)	2.601 (0.0130)	-0.285 (0.7769)
Microhabitat Twigs	-	-	-	0.059 (0.9531)	4.305 (0.0001)	-0.170 (0.8657)
Diet Insectivorous	-	-	-	-2.406 (0.0208)	0.941 (0.3522)	0.689 (0.4951)
Diet Omnivorous	-	-	-	-2.115 (0.0407)	1.441 (0.1573)	1.154 (0.2555)
Parity Viviparous	-	-	-	0.263 (0.7937)	-0.725 (0.4730)	-0.488 (0.6282)
Model statistics	λ=0.540 $F_{1,49}$=8.825 p=0.0046 R^2=0.153	λ=0.813 $F_{1,49}$=1.414 p=0.2402 R^2=0.028	λ=0.526 $F_{1,49}$=0.150 p=0.7006 R^2=0.003	λ=0.212 $F_{9,40}$=3.911 p=0.0013 R^2=0.468	λ=0.708 $F_{9,40}$=3.23 p=0.0049 R^2=0.421	λ=0.414 $F_{9,40}$=1.028 p=0.435 R^2=0.188

Table 11: AIC results for PGLS models for PC axes 1-3.

	PC1	PC2	PC3
Model 1 (PC axis~SVL+Microhabitat+Diet+Parity)	-289.42	-279.1031	-331.9155
Model 2 (PC axis~Microhabitat+Diet+Parity)	-282.5922	-272.5446	-332.691
Model 3 (PC axis~SVL+Diet+Parity)	-279.4273	-265.1745	-334.3322
Model 4 (PC axis~SVL+Microhabitat+Parity)	-287.2845	-280.1522	-333.818
Model 5 (PC axis~SVL+Microhabitat+Diet)	-291.3466	-280.48	-333.6298

Figure 1: Examples of Liolaemus lizard species and their microhabitats. From top to bottom, species are *L. filiorum* (and its boulder microhabitat in the Andes), *L. nigromaculatus* and its sandy microhabitats in Atacama), *L. melaniceps* (and its rocky environments in central Chile), and *L. nigriceps* (and its open and bushy microhabitats in the high Andes plateau). All pictures taken by D. Pincheira-Donoso.

Figure 2: Location of landmarks placed on a specimen of *Liolaemus kolengh*.

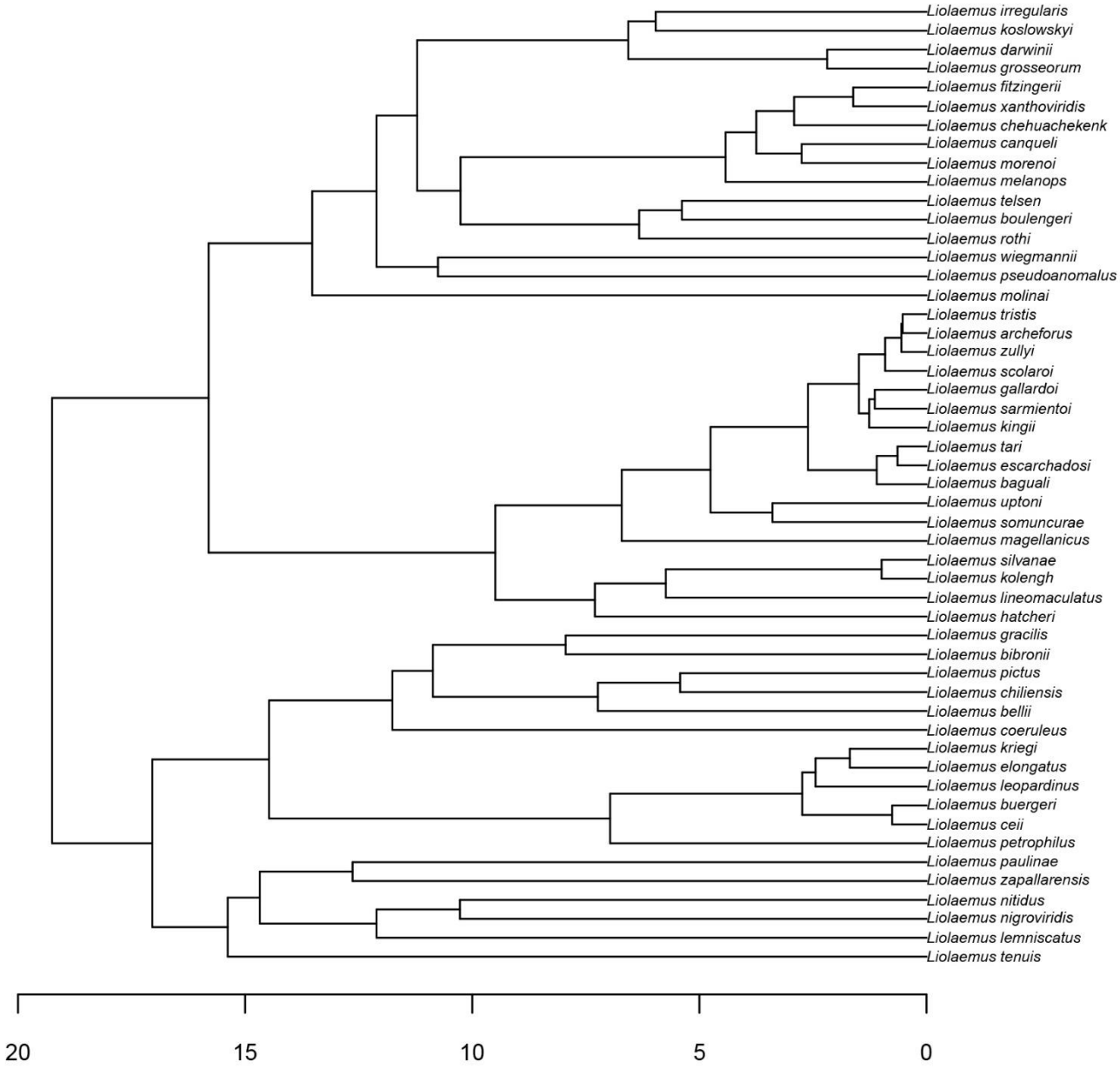


Figure 3: Phylogenetic tree of 51 of the Liolaemus species included in this study. Time scale is in millions of years.

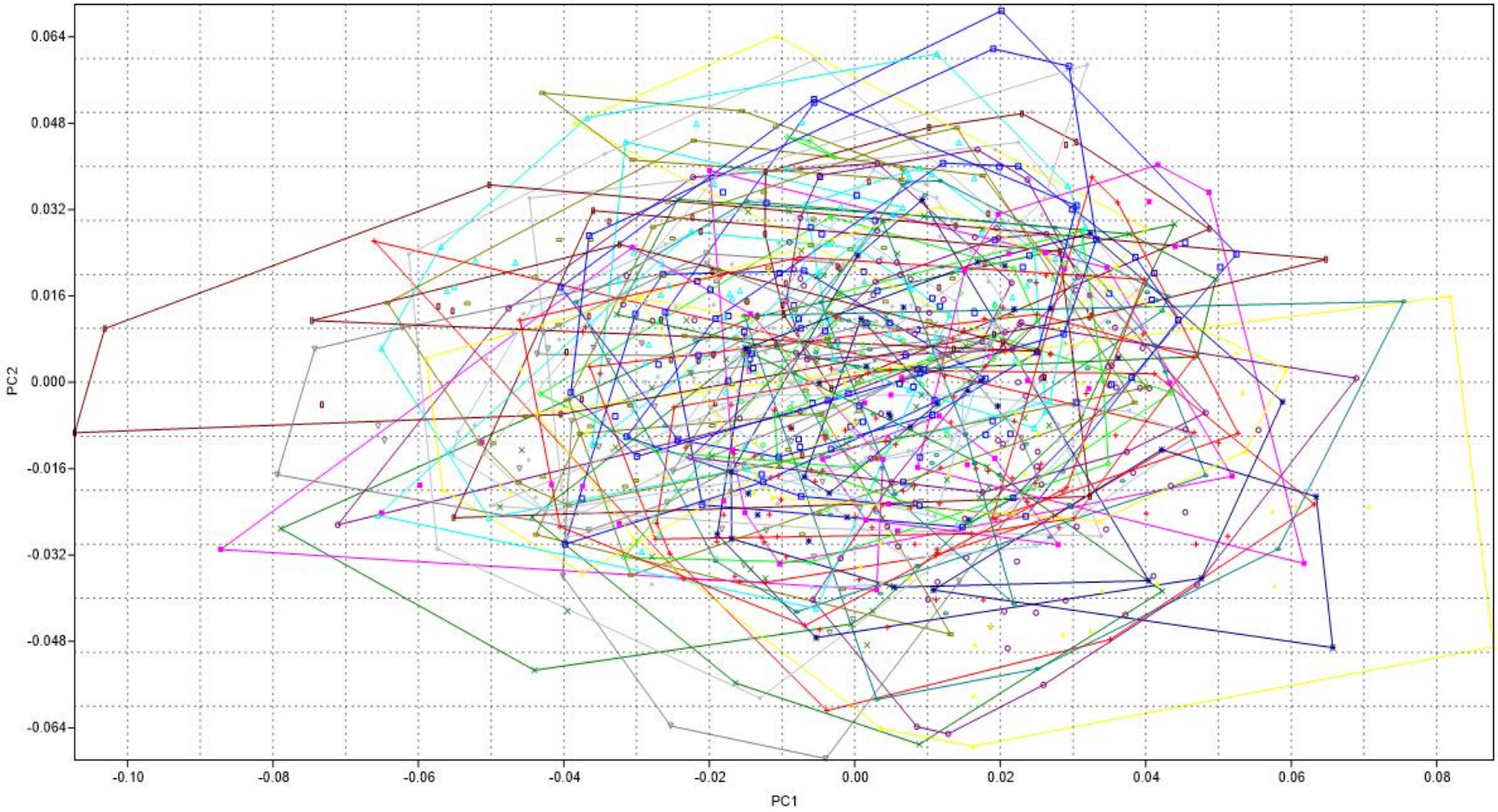


Figure 4: The pattern of distribution for all specimens included in the study, across all 62 species and both sexes, within morphospace using the first two PC axes. Each convex hull denotes a species.

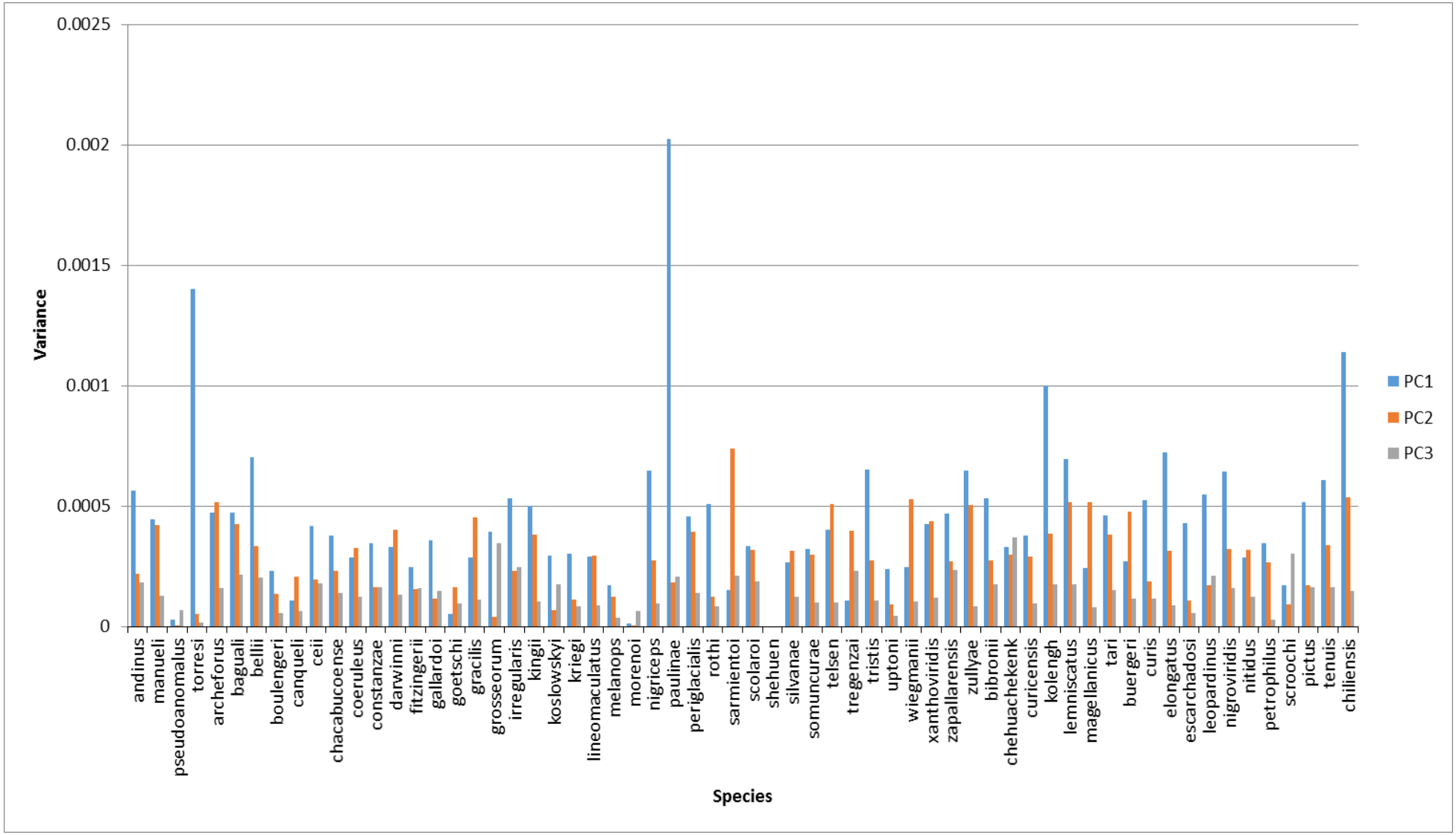


Figure 5: Within-species variation for PC1, PC2 and PC3 for each species. Each bar shows the amount of individual variance that occurs within that species for the respective PC axis. Variance calculated using the function VAR.S in Excel.

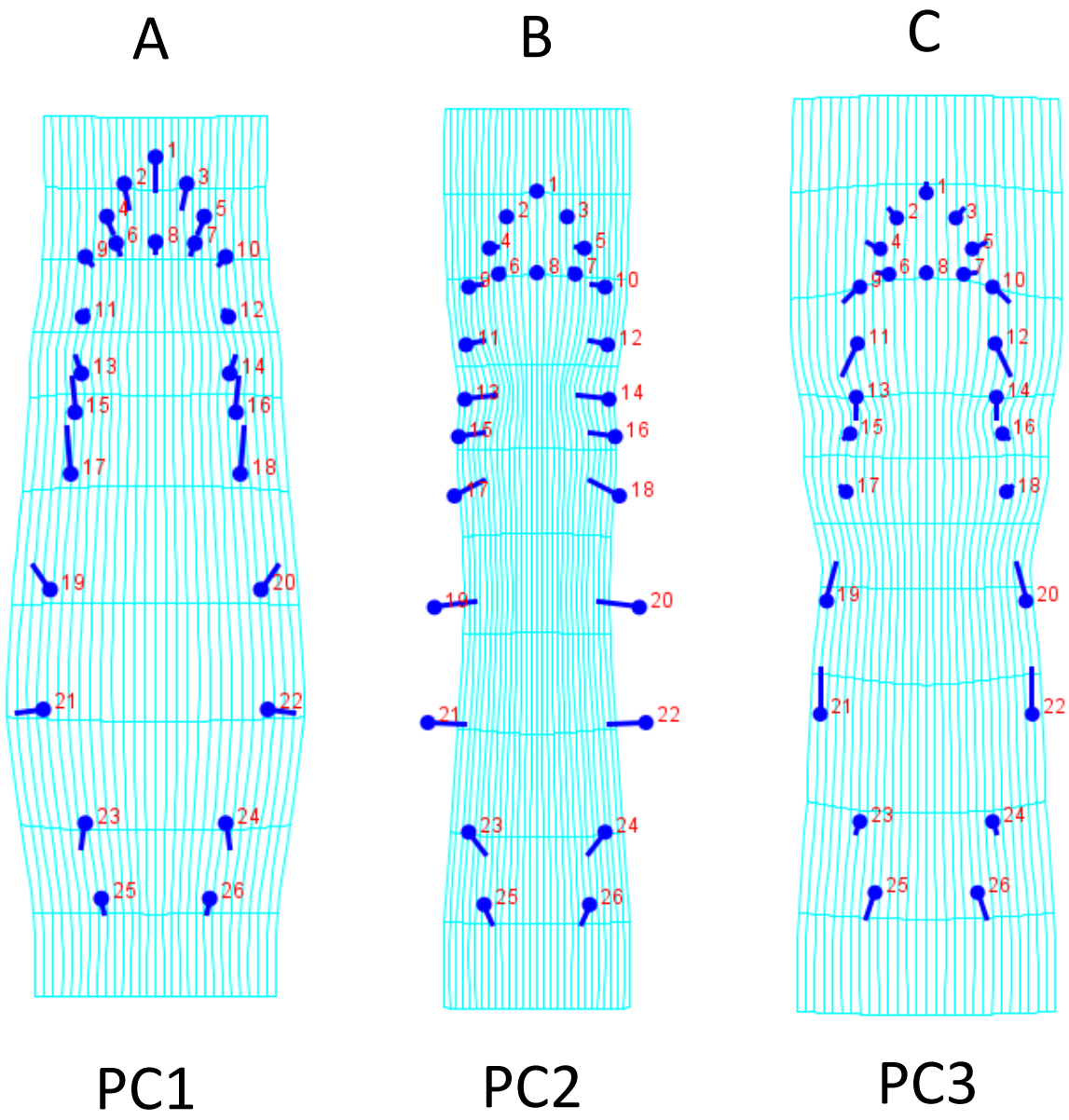


Figure 6: Deformation grids representing the first three principal component axes showing the mean configuration of shape and the direction and magnitude of change from the mean, as well as the change of size of a region relative to other regions.

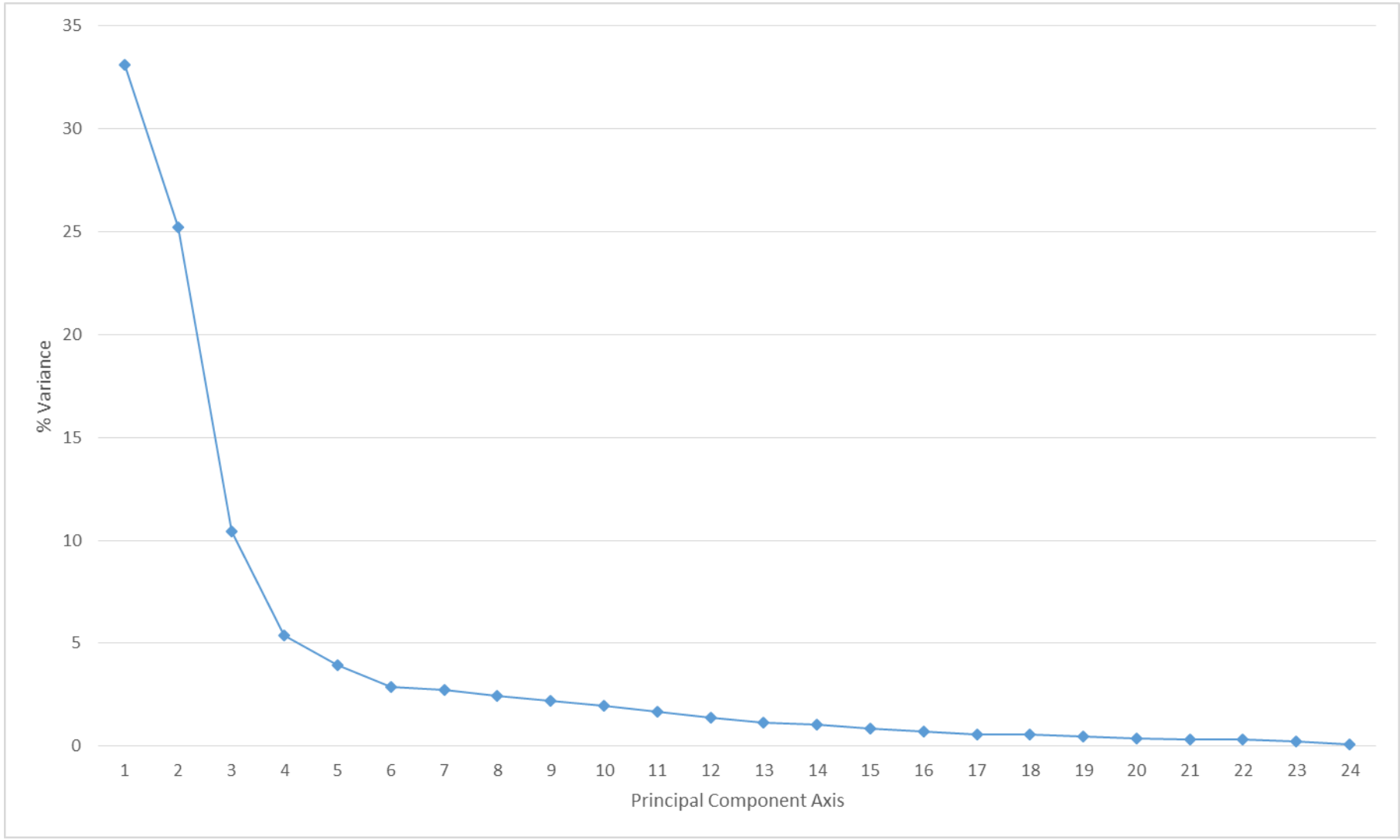


Figure 7: Scree plot showing amount of variance explained in each principal component axis based on eigenshape analysis.

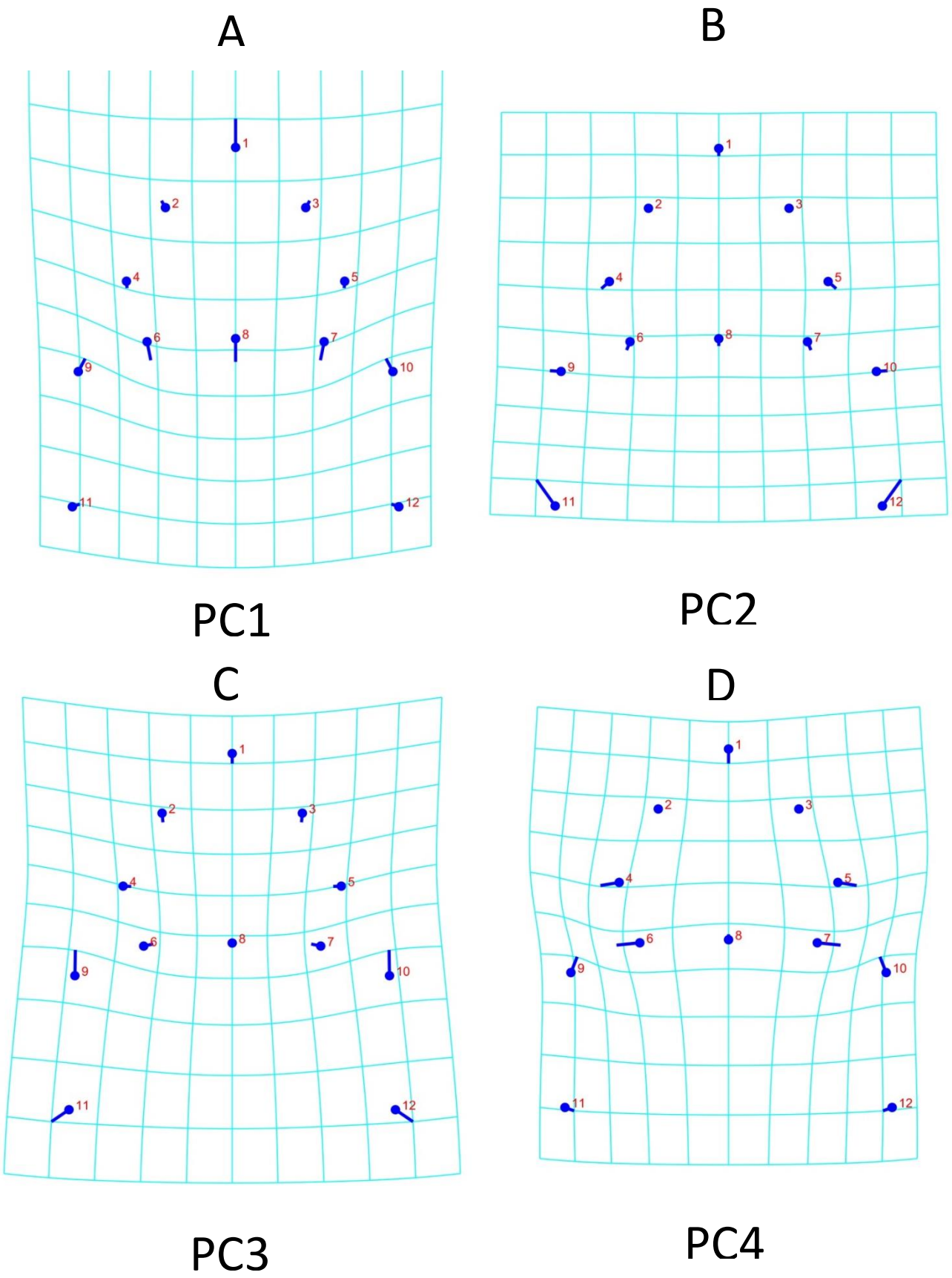


Figure 8: Deformation grids representing the first four principal component axes for the head, showing the mean configuration of shape and the direction and magnitude of change from the mean, as well as the change of size of a region relative to other regions.

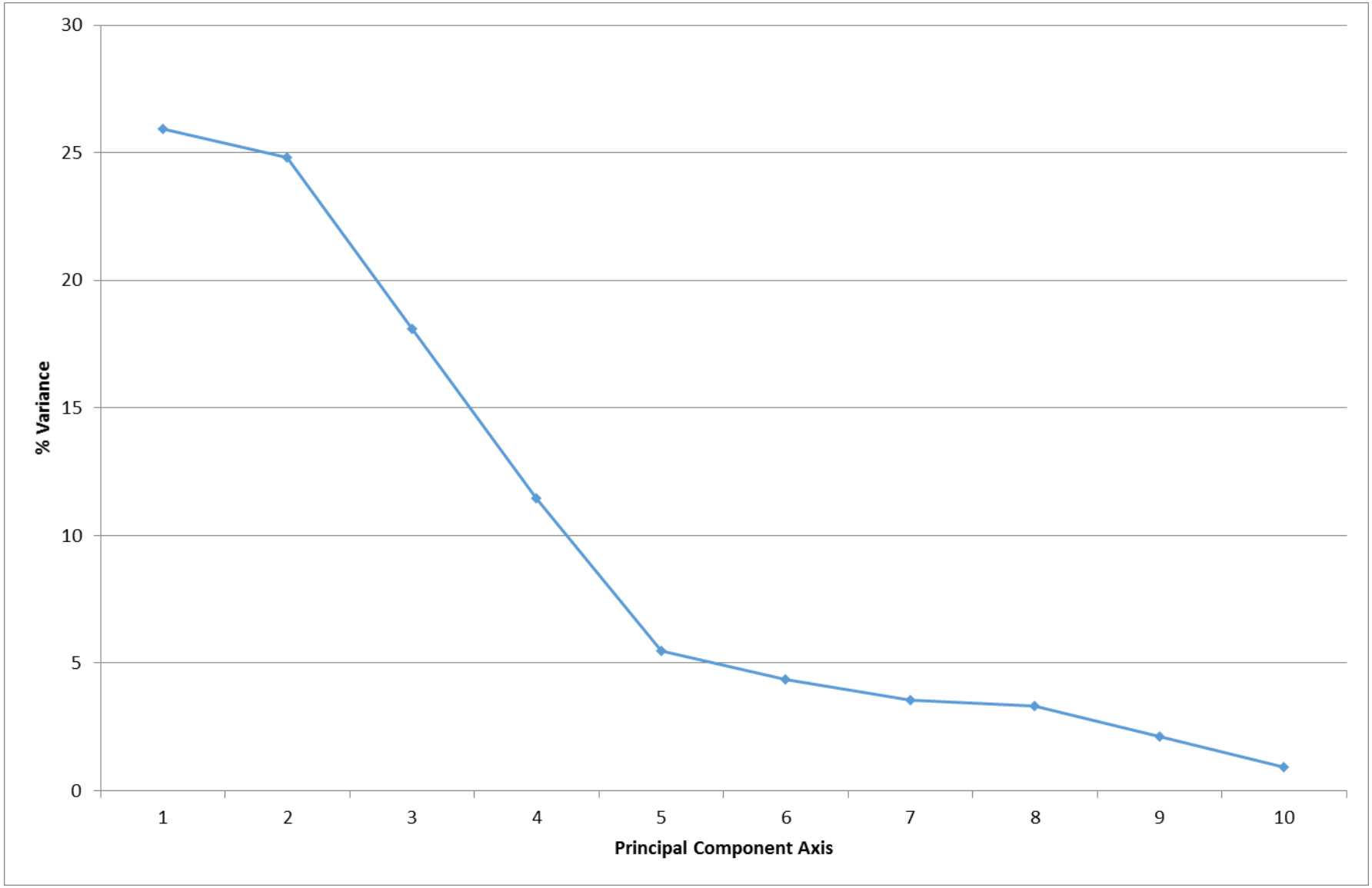


Figure 9: Scree plot showing amount of variance explained in each principal component axis based on eigenshape analysis for the head.

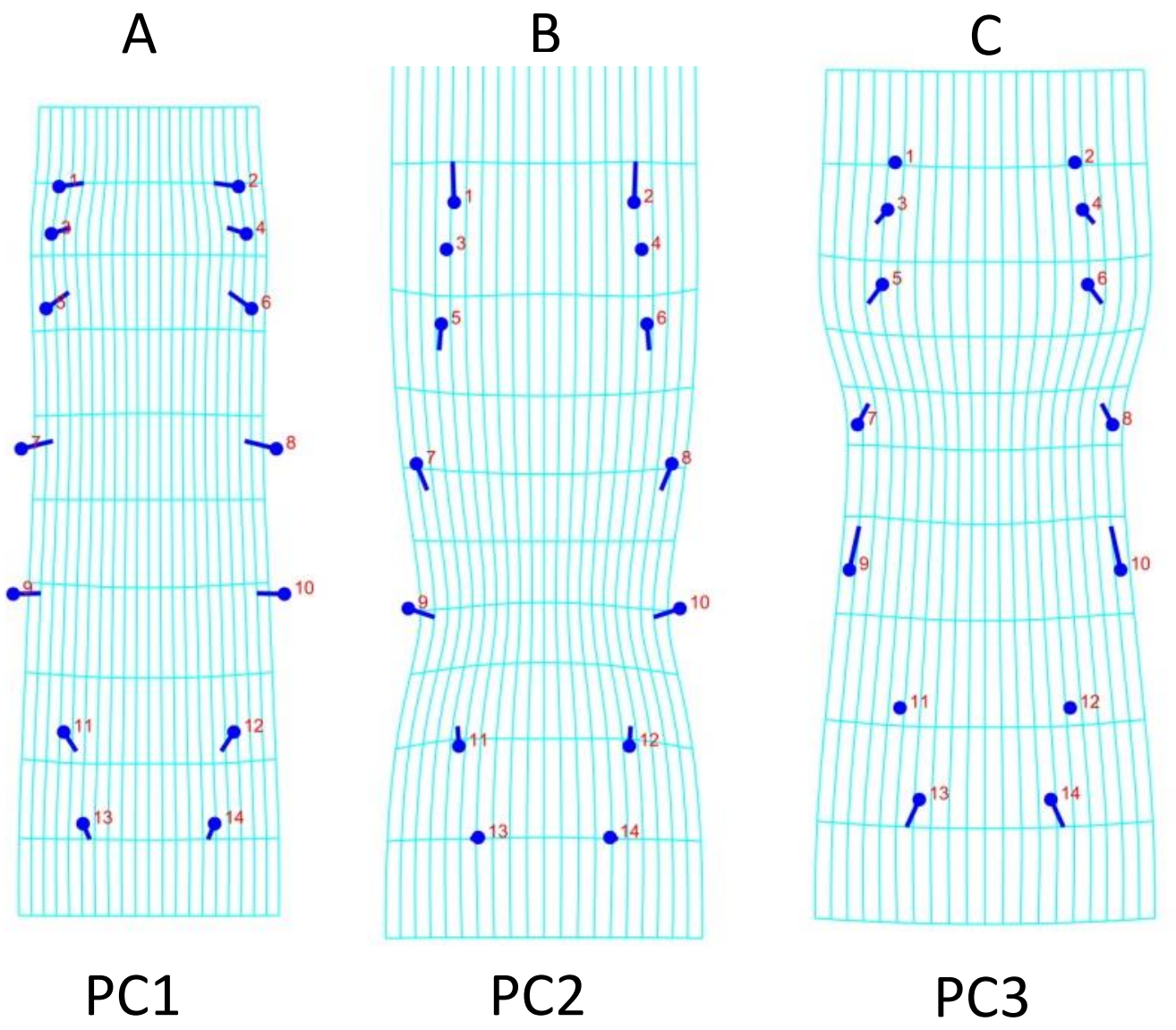


Figure 10: Deformation grids representing the first three principal component axes (left to right) for the body, showing the mean configuration of shape and the direction and magnitude of change from the mean, as well as the change of size of a region relative to other regions.

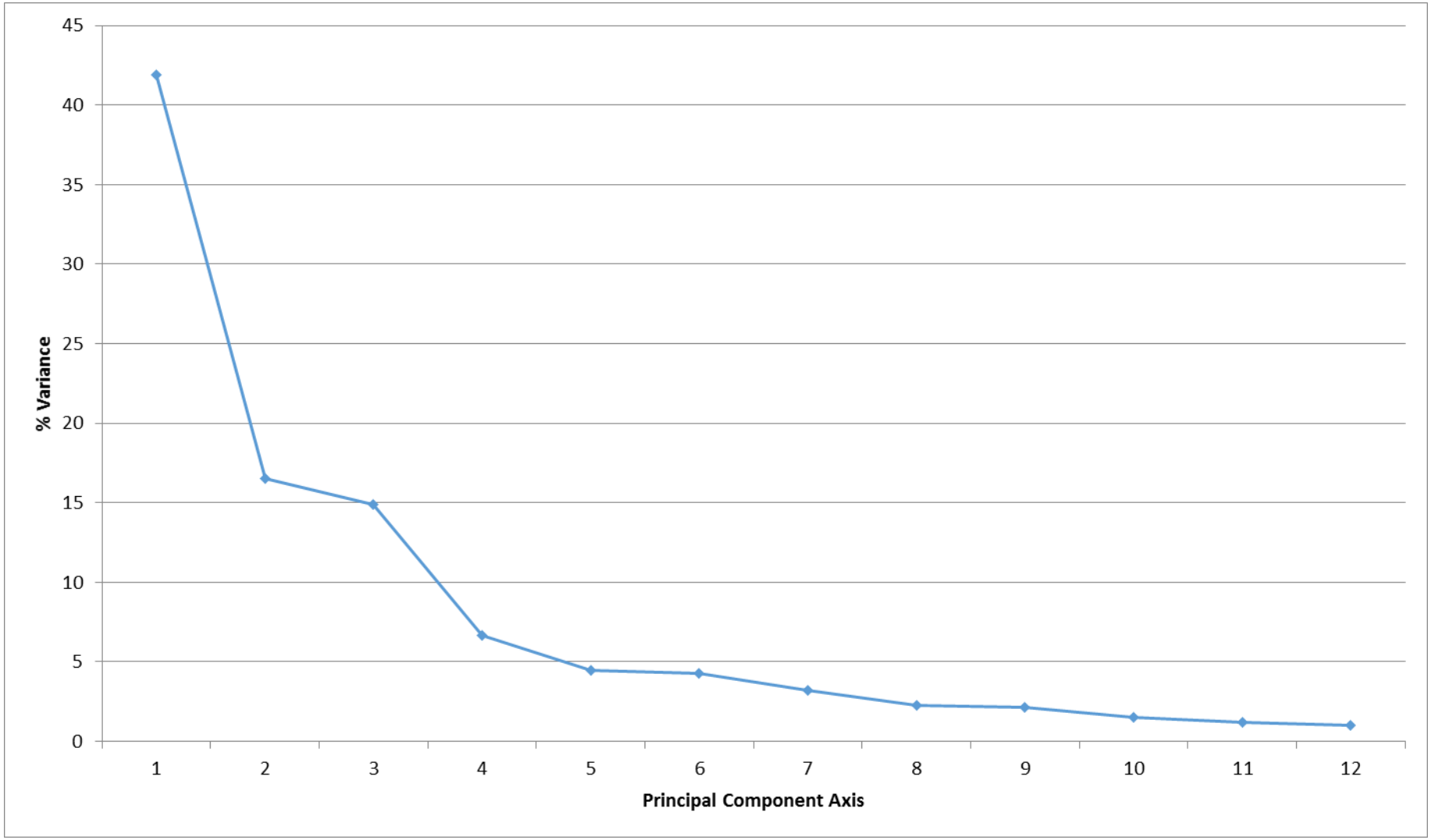
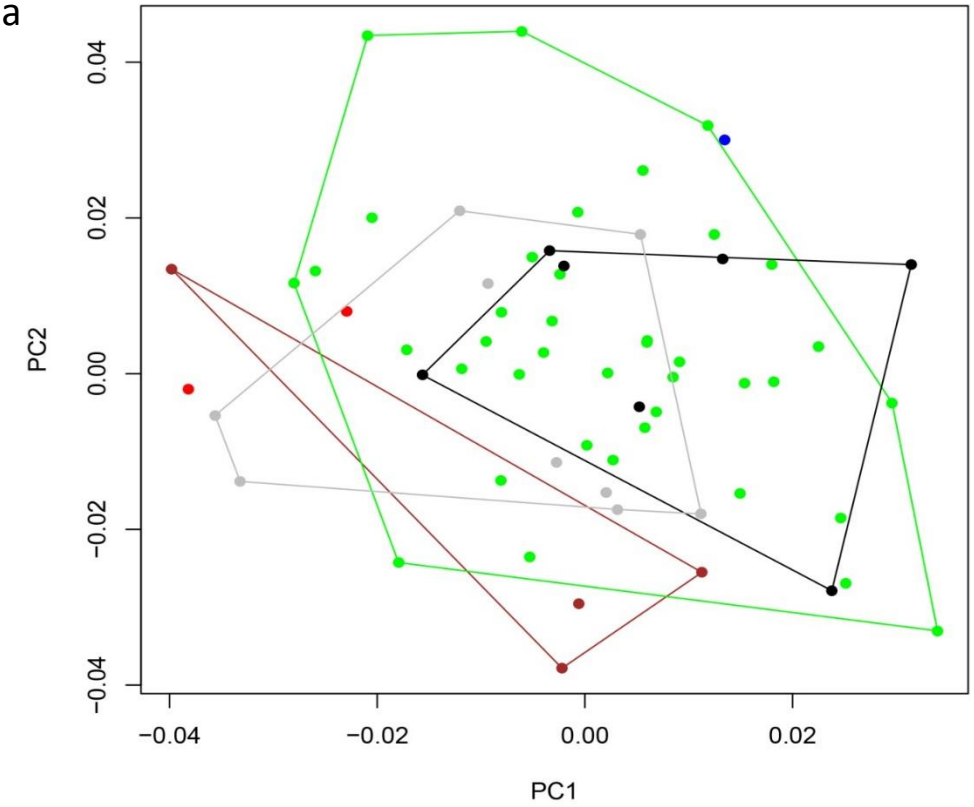


Figure 11: Scree plot showing amount of variance explained in each principal component axis based on eigenshape analysis for the body.

12a



12b

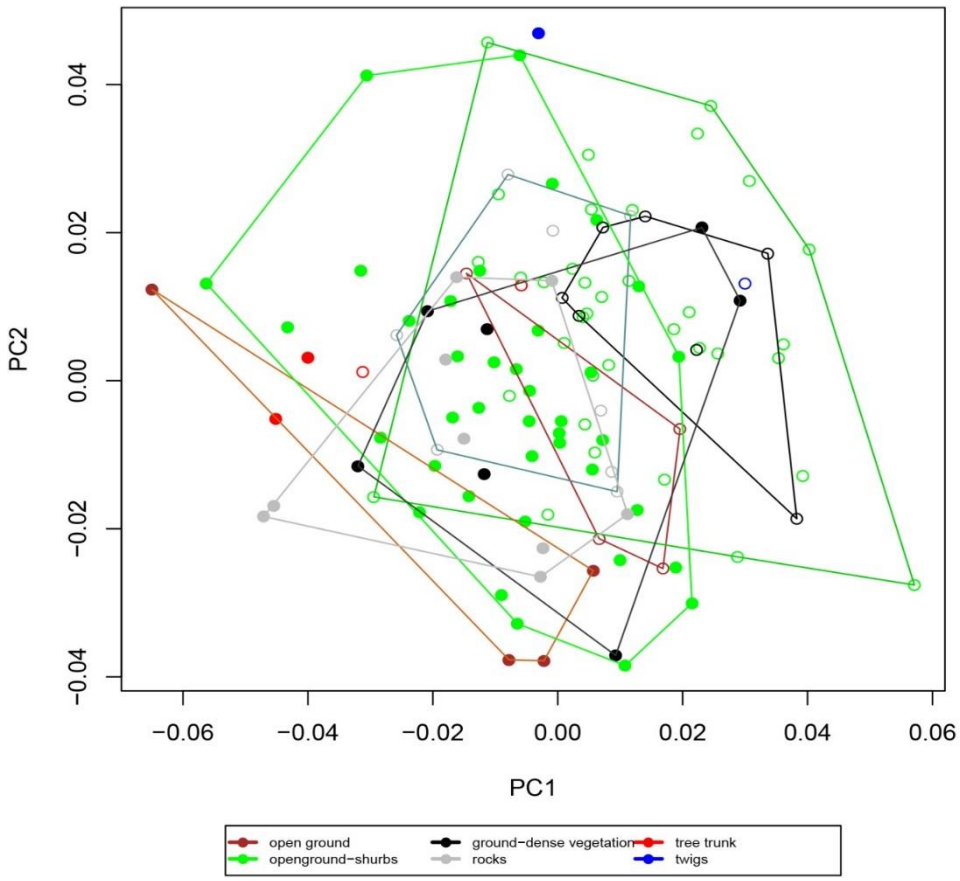


Figure 12a (top): Morphospace plot of species averages of the whole body, convexhulls denote microhabitat category. Figure 12b (bottom): Morphospace plot of male averages (closed circles) and females (open circles) of the whole body, convexhulls denote microhabitat category and sex.

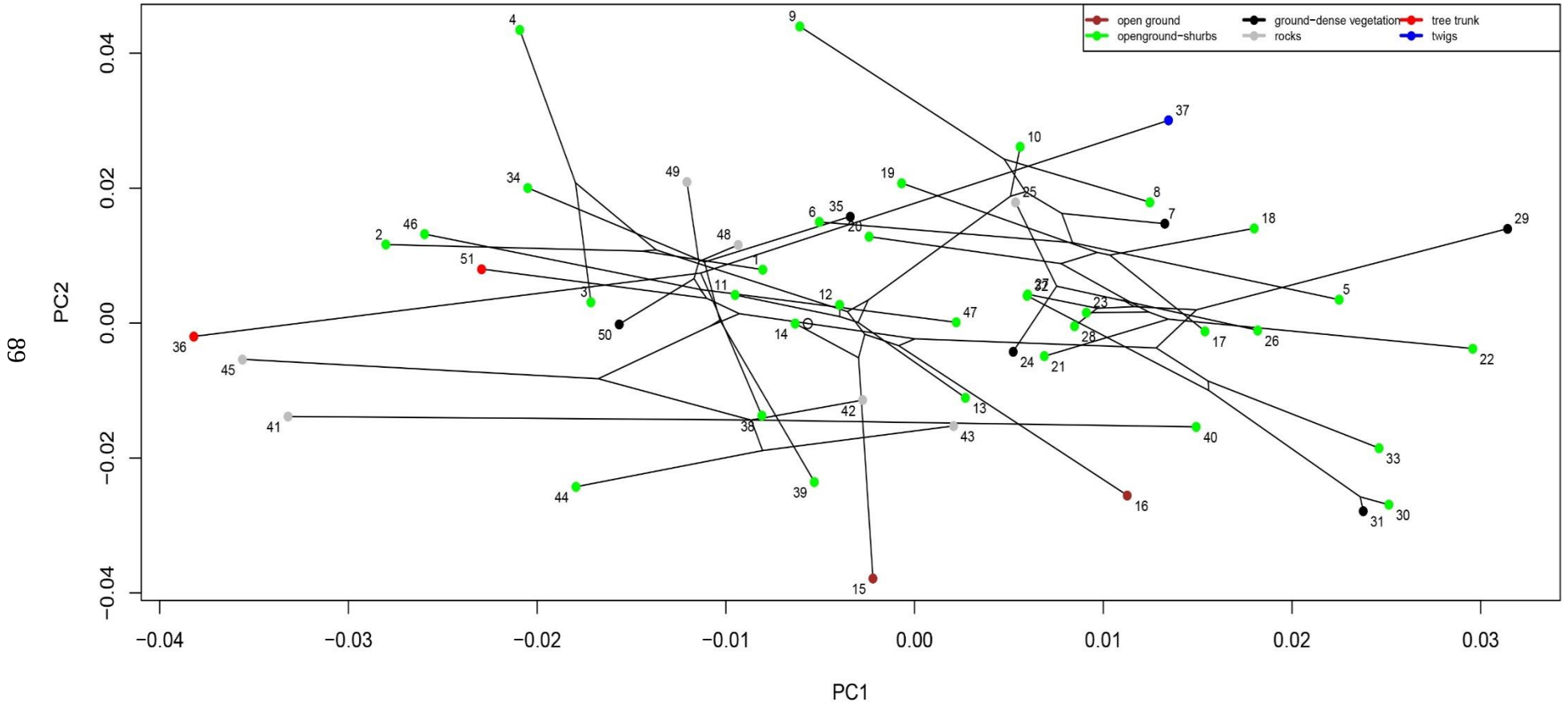


Figure 13: Phylomorphospace for PC1 and PC2 showing the location of species' average body shape overlaid with the phylogeny. Internal nodes mark the estimated morphology of ancestor species. Branch lengths do not represent time since split, but distance in morphospace.

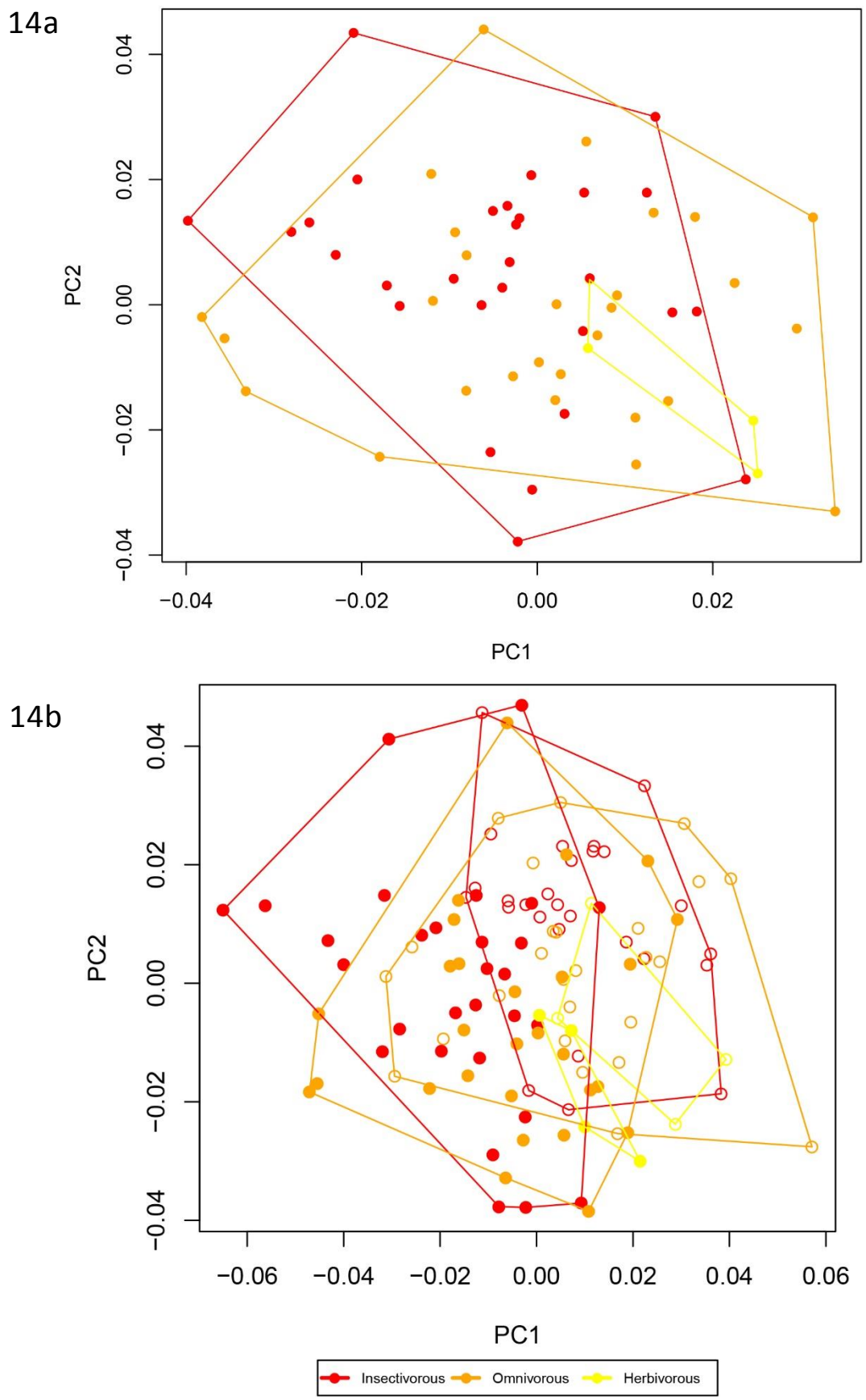


Figure 14a (top): Morphospace plot of species averages, convex hulls denote diet. Figure 14b (bottom): Morphospace plot of male averages (closed circles) and females (open circles), convex hulls denote diet and sex.

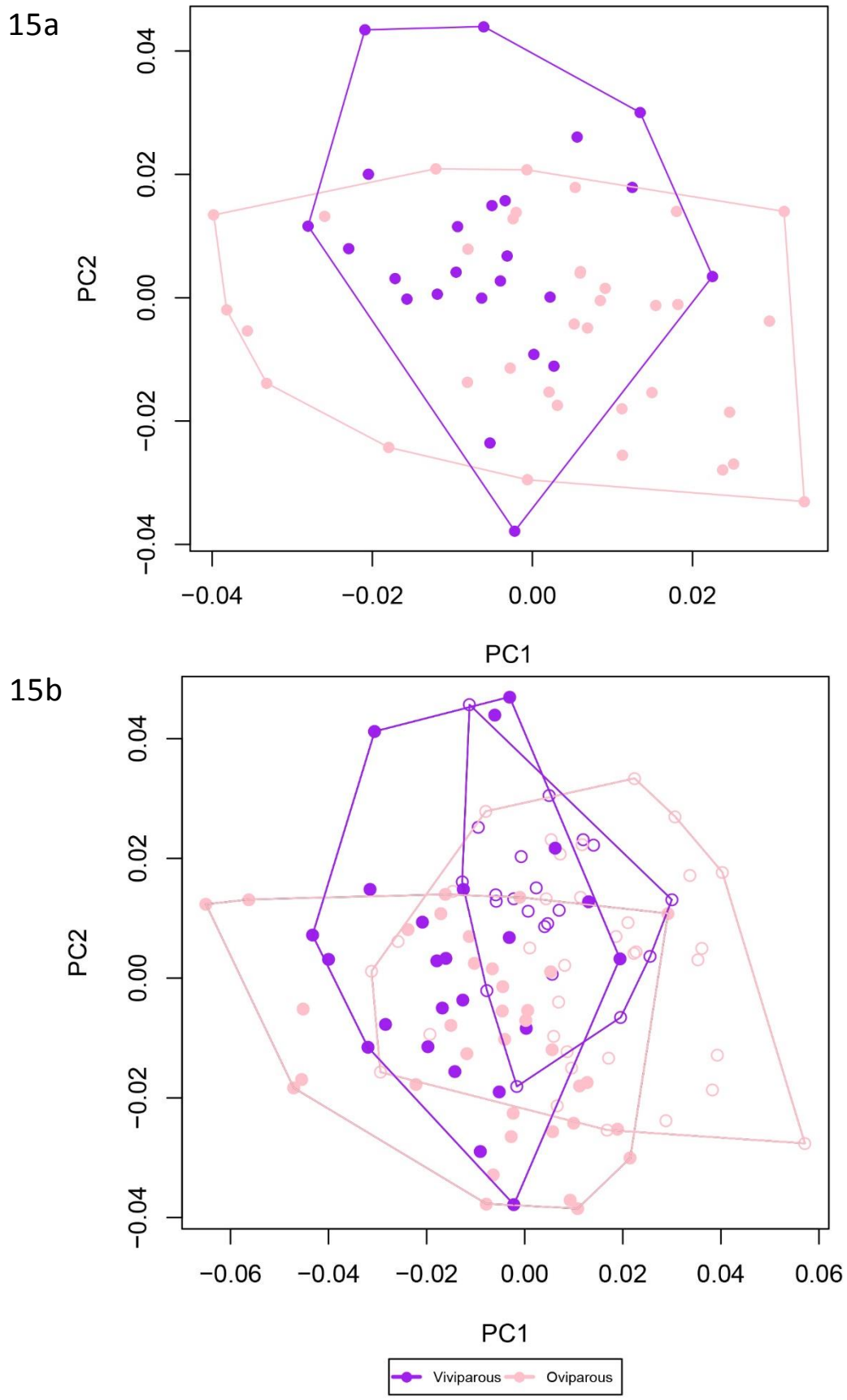


Figure 15a (top): Morphospace plot of species averages for the entire specimen, convex hulls denote parity mode. Figure 15b (bottom): Morphospace plot of male averages (closed circles) and female averages (open circles) for the entire specimens, convex hulls denote parity mode and sex.

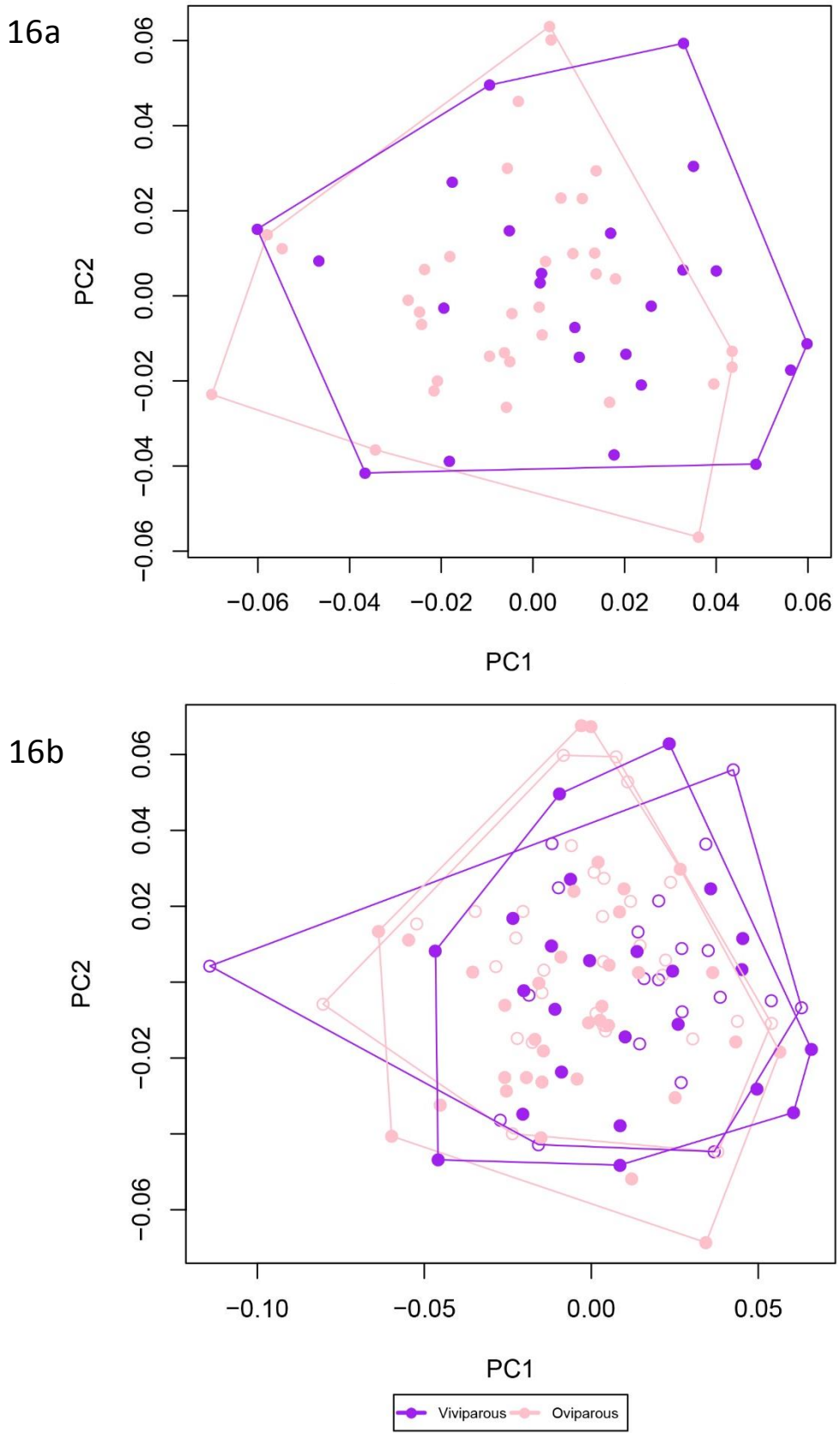


Figure 16a (top): Morphospace plot of species averages for the head only, convex hulls denote parity mode. Figure 16b (bottom): Morphospace plot of male averages (closed circles) and female averages (open circles) for the head only, convex hulls denote parity mode and sex.

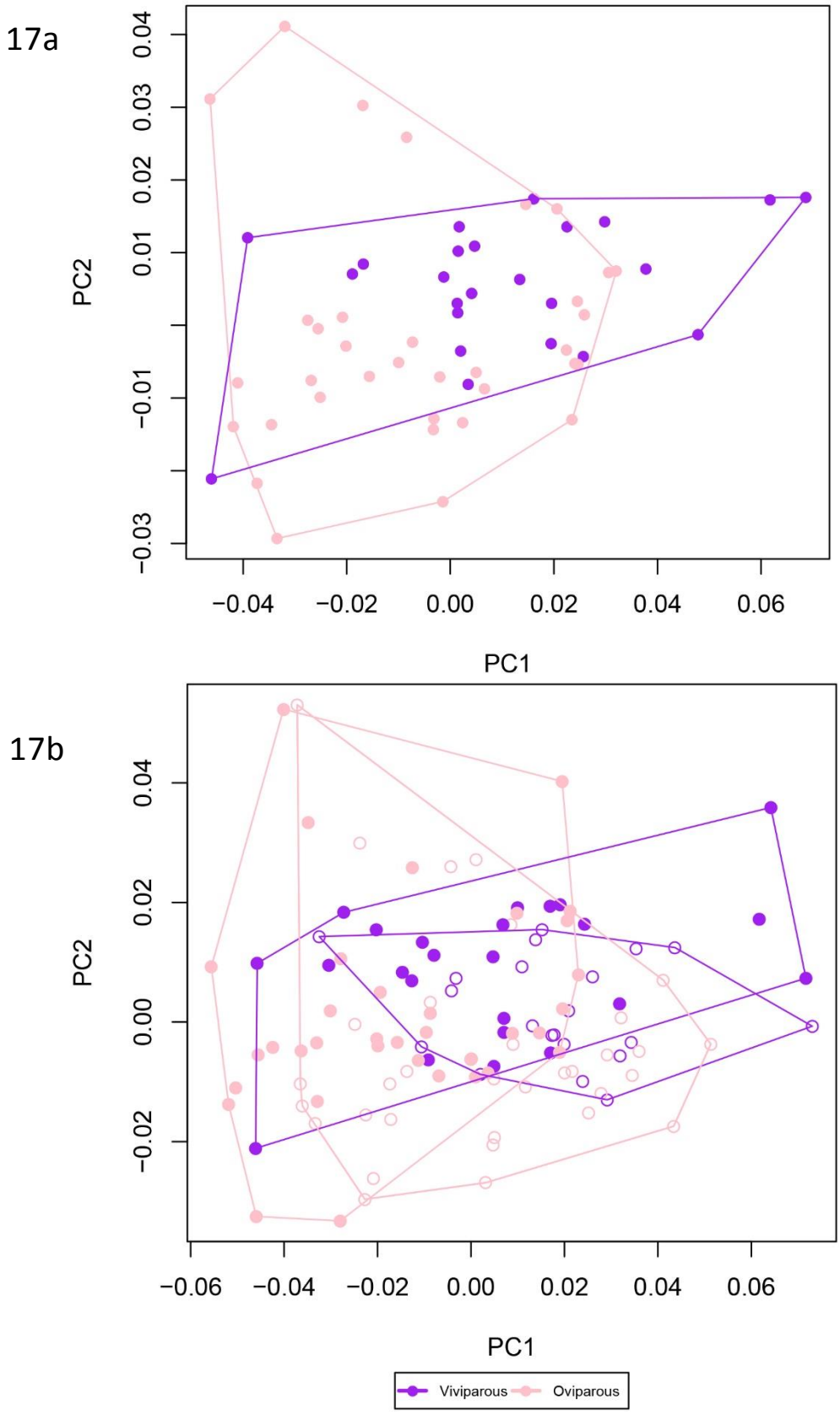


Figure 17a (top): Morphospace plot of species averages for the body only, convexhulls denote parity mode. Figure 17b (bottom): Morphospace plot of male averages (closed circles) and female averages (open circles) for the body only, convex hulls denote parity mode and sex.

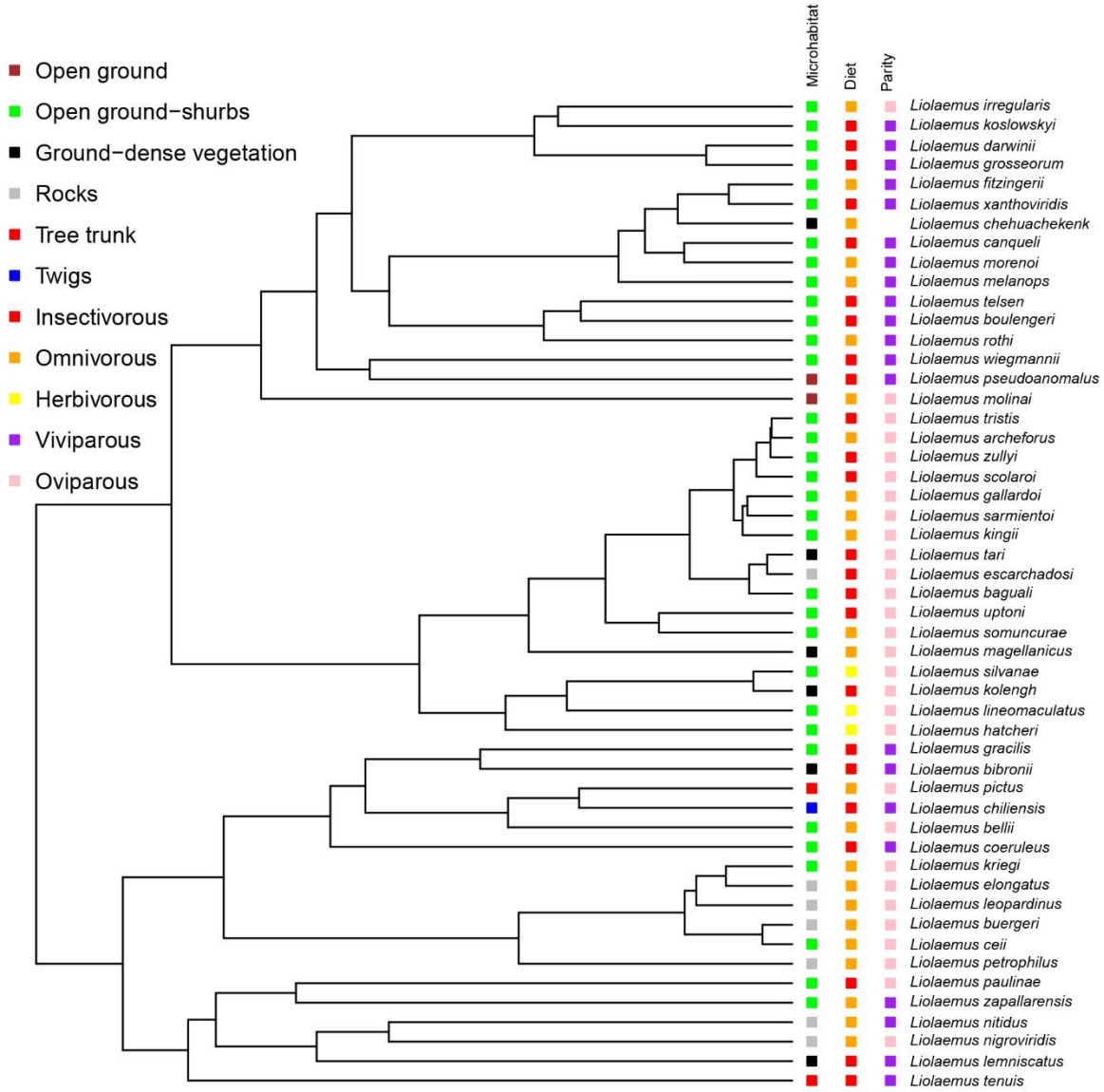


Figure 18: Phylogeny with coloured markers depicting the spread of microhabitat, diet and parity mode across the phylogenetic tree. *Liolaemus chehuachekenk* is left blank in the parity column as parity mode is unknown.

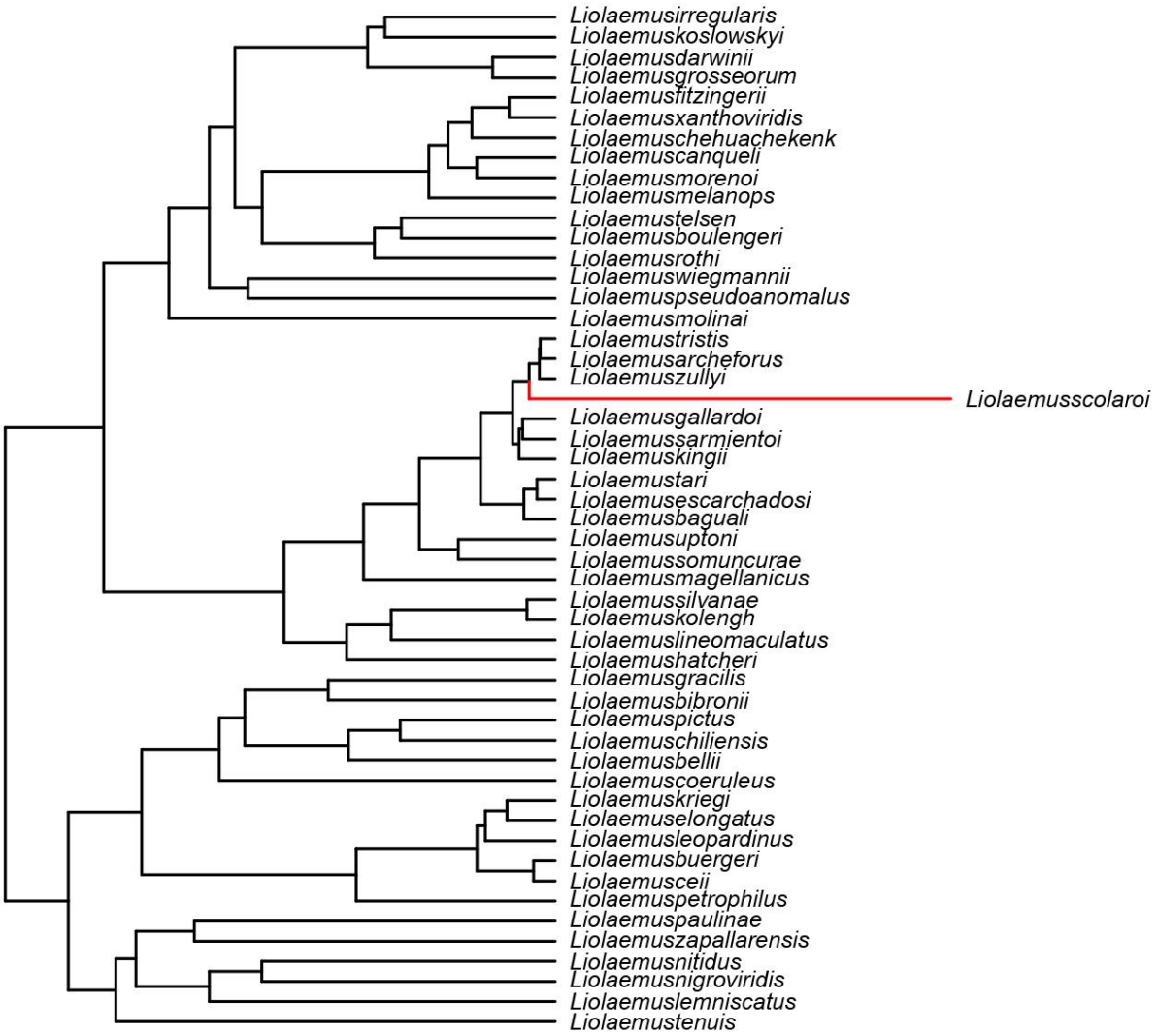


Figure 19: Shifts of phenotypic rate evolution for SVL, species with an increased branch length, shown in red, experience rates of evolution higher than expected under Brownian motion.

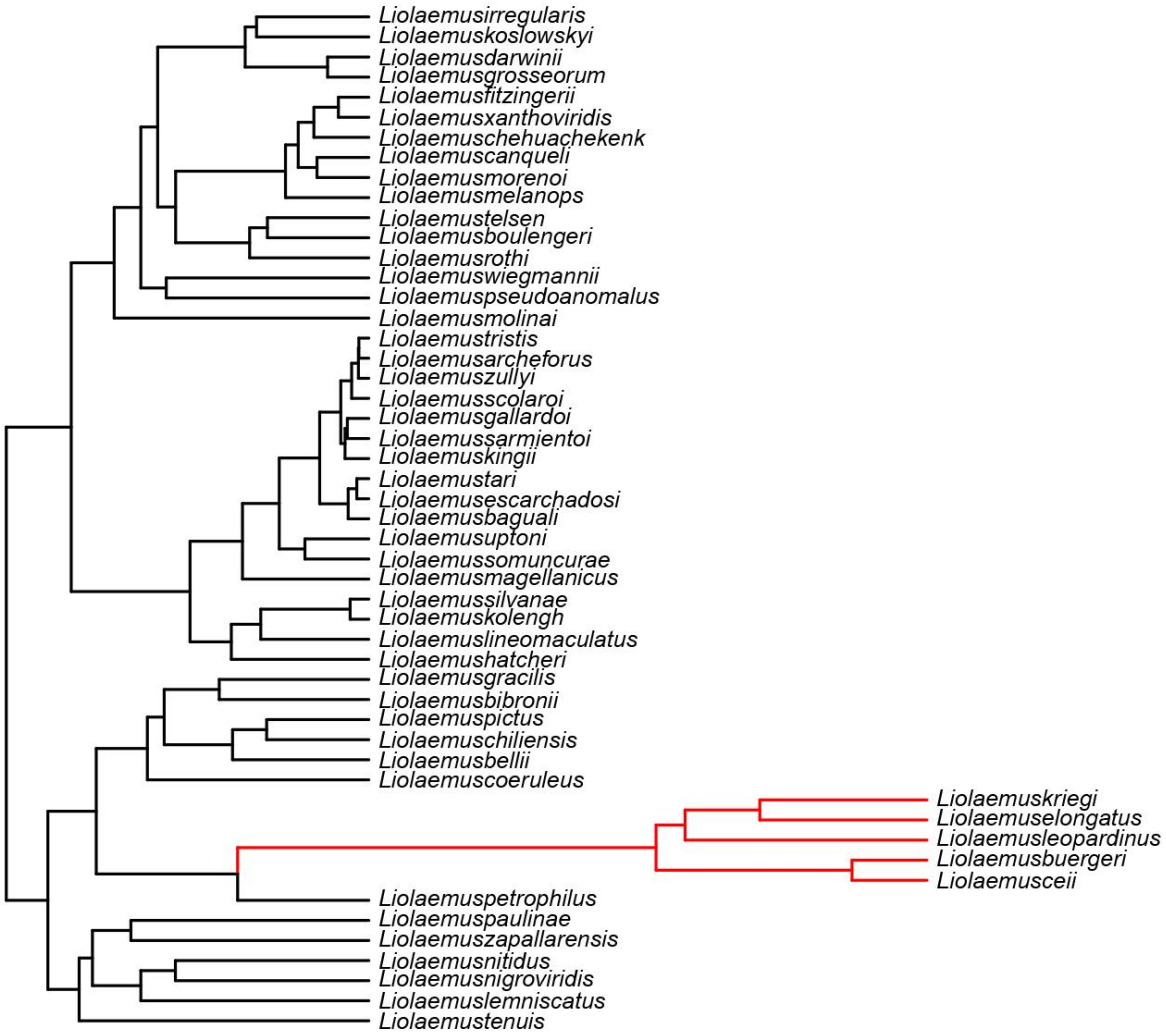


Figure 20: Shifts of phenotypic rate evolution for PC1, species with an increased branch length, shown in red, experience rates of evolution higher than expected under Brownian motion.

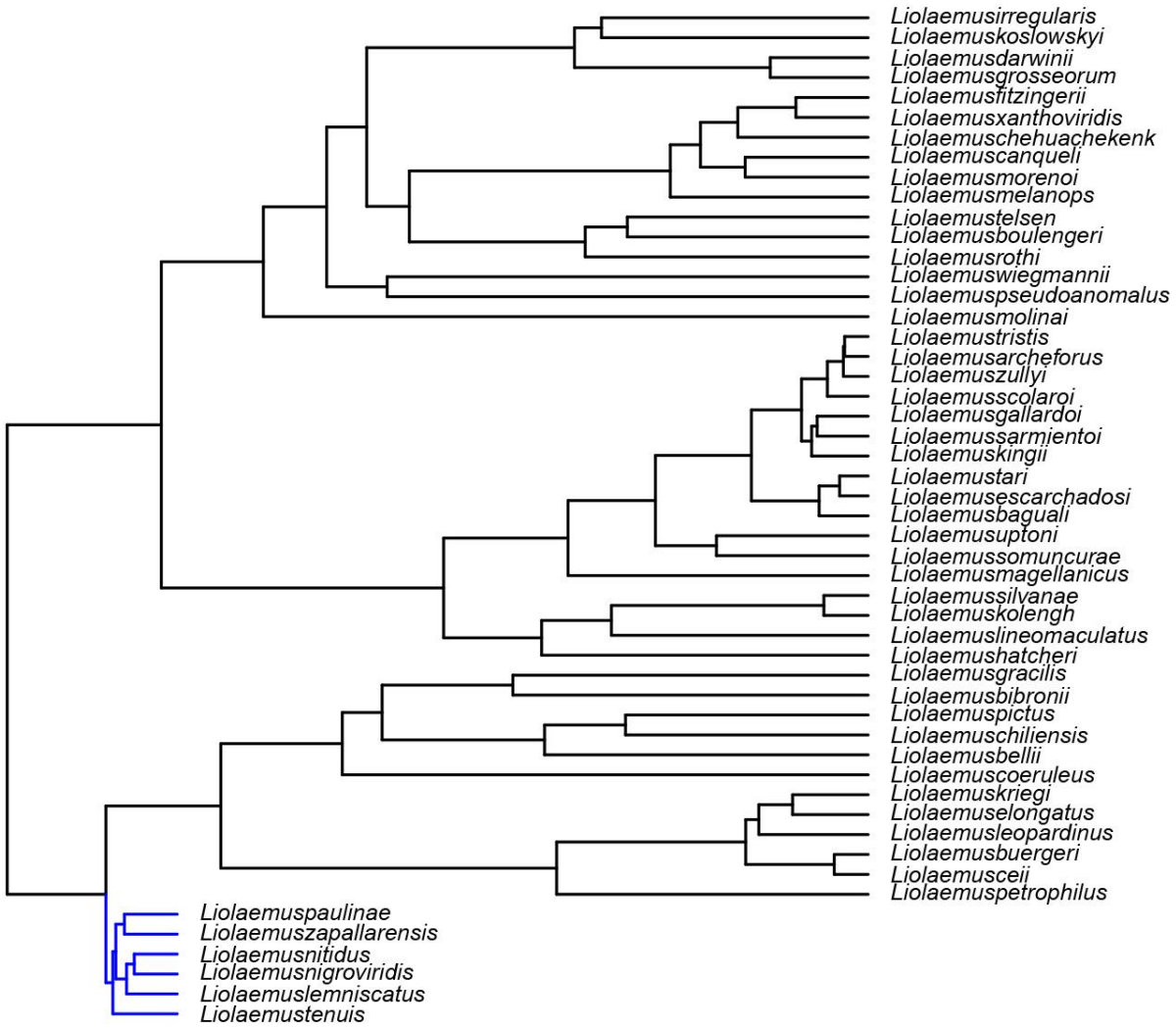


Figure 21: Shifts of phenotypic rate evolution for PC2, species with a decreased branch length, shown in blue, experience rates of evolution lower than expected under Brownian motion.

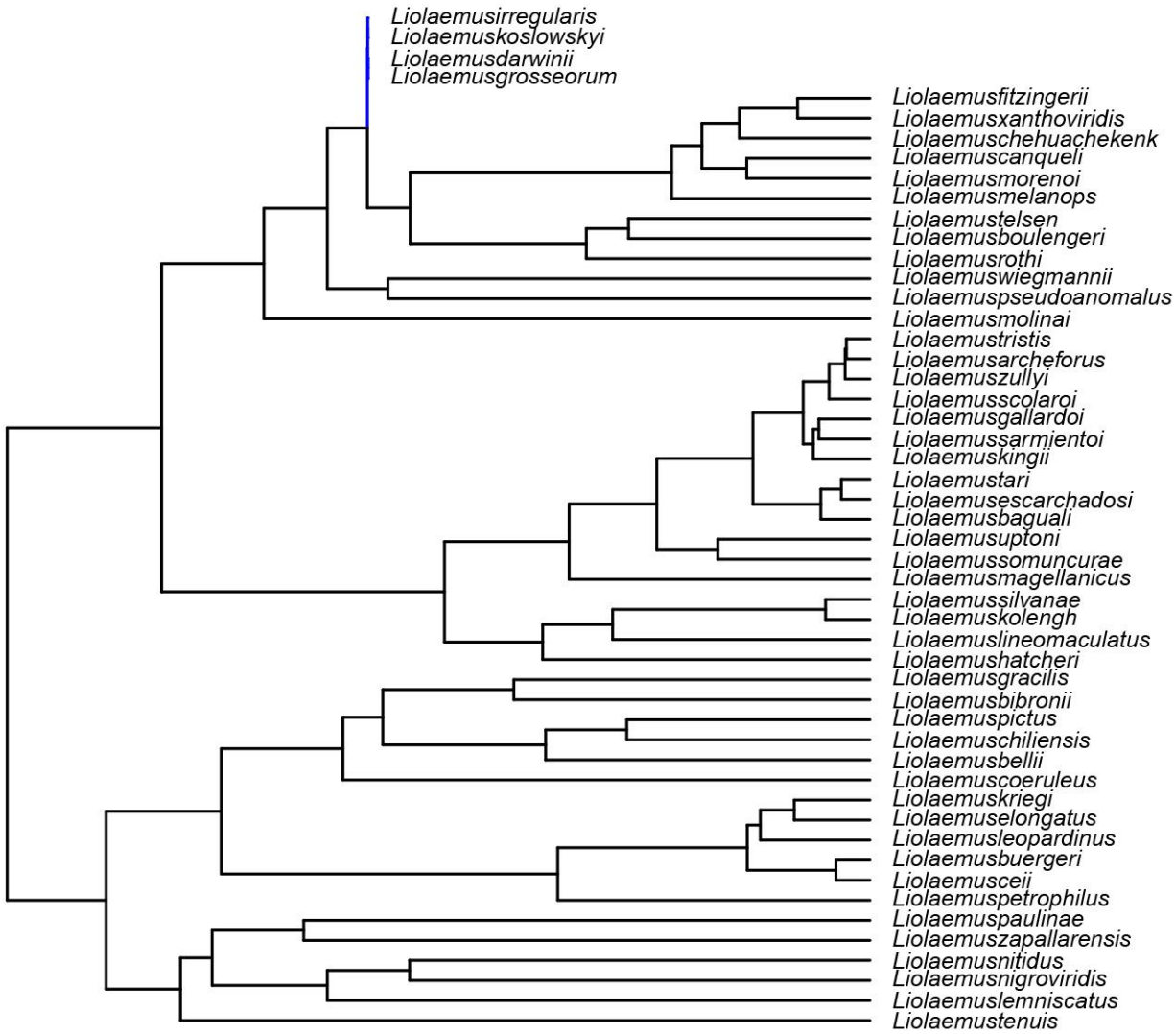


Figure 22: Shifts of phenotypic rate evolution for PC3, species with a decreased branch length, shown in blue, experience rates of evolution lower than expected under Brownian motion.

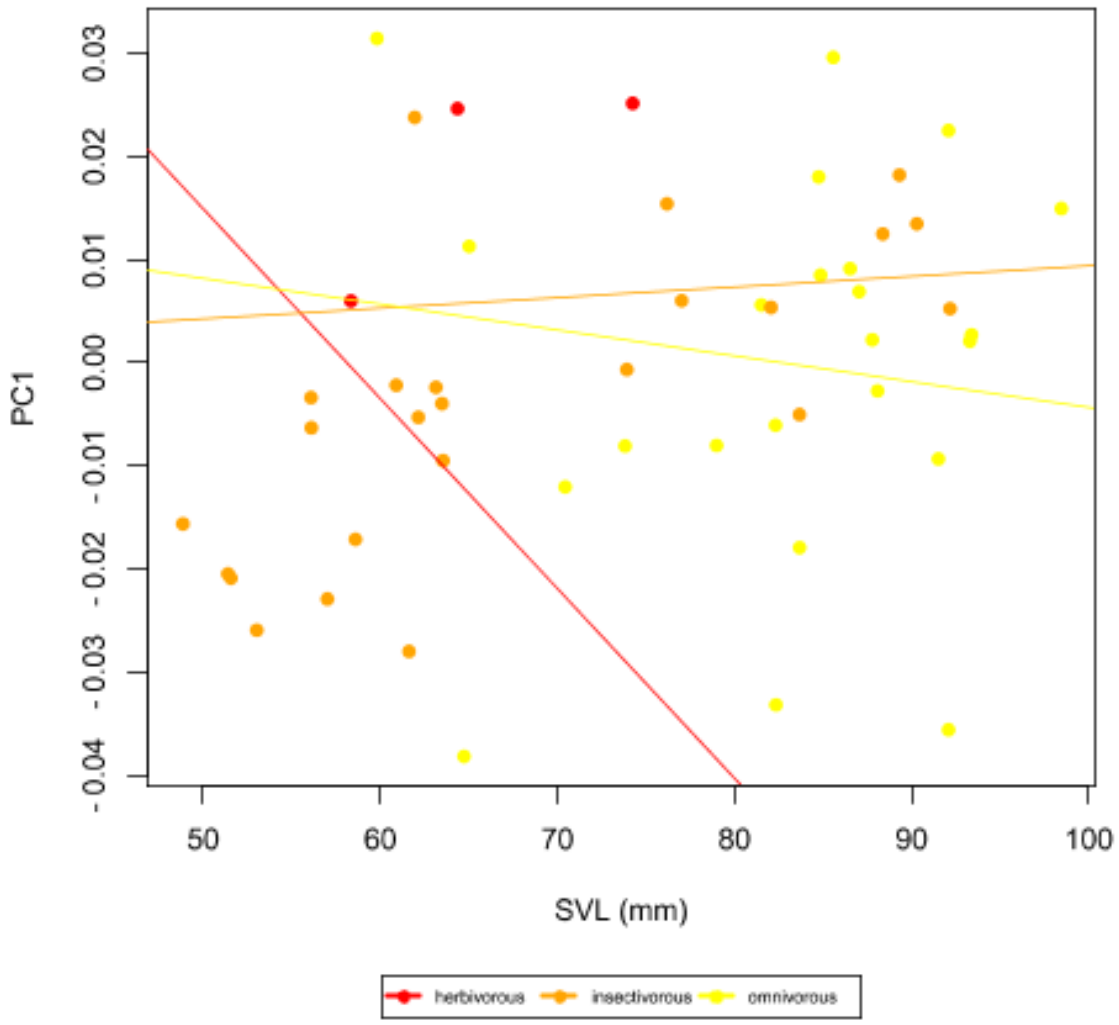


Figure 23: Body size (SVL) and PC2, using species averages, lines show relationship between SVL and PC2 within each diet category.

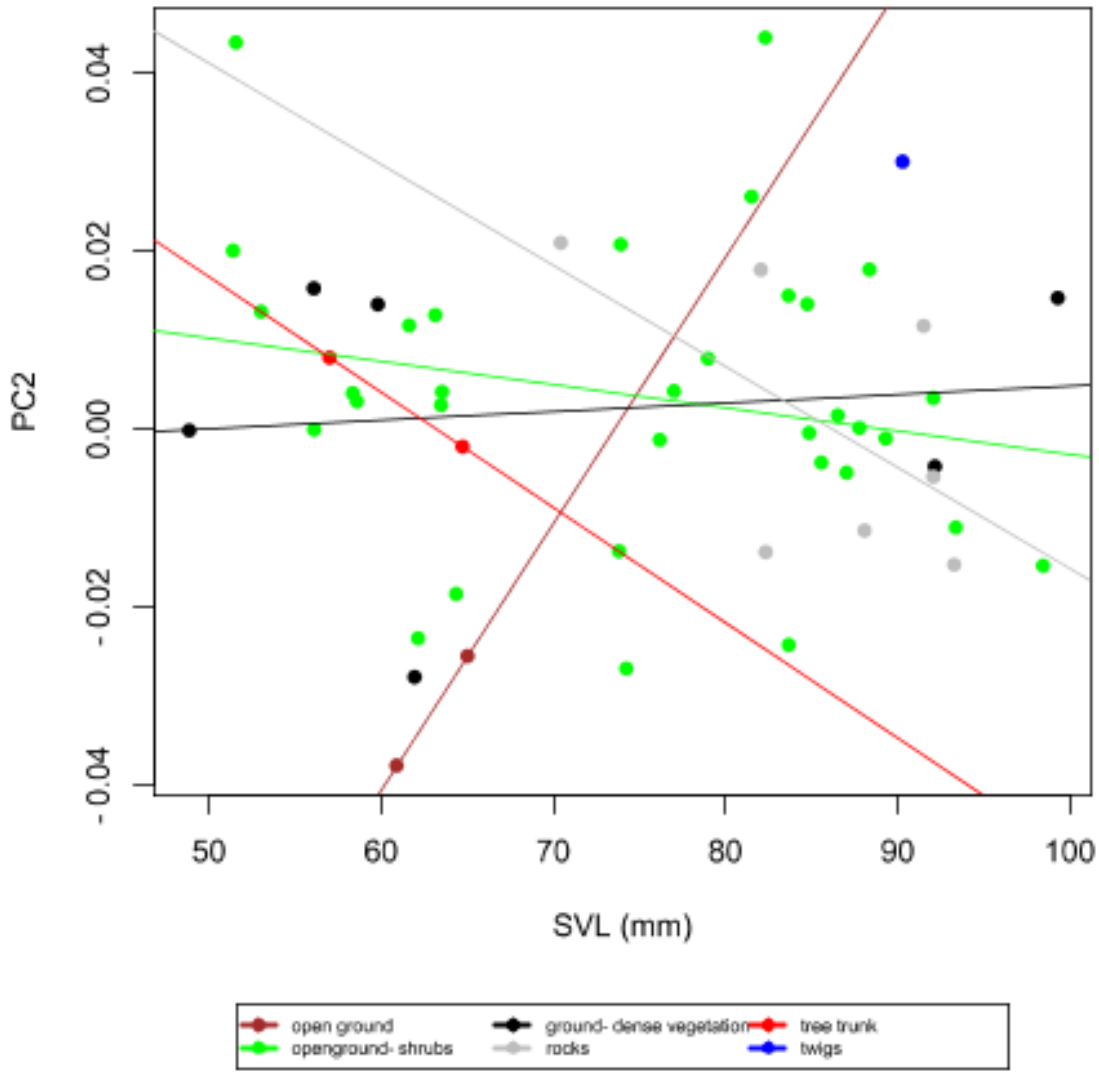


Figure 24: Body size (SVL) and PC2, using species averages, lines show relationship between SVL and PC2 within each microhabitat category.

8 Appendix

NPMANOVA p values, showing which species are significantly separated, using PC1 and PC2. Values highlighted in grey are signi ficantly different, showing that interspecific variation is greater than intraspecific variation in these species.

	andinus	archeforus	baguali	bellii	bibronii	boulengeri	buergeri	canqueli	ceii	chacabucoense	chehuachekenk	chiliensis
andinus		0.0001	0.0023	0.0004	0.0001	0.0001	0.0594	0.0001	0.0026	0.0001	0.0001	0.0001
archeforus	0.0001		0.0783	0.0001	0.0001	0.0023	0.0008	0.6472	0.0001	0.0219	0.6764	0.1414
baguali	0.0023	0.0783		0.0065	0.0005	0.0255	0.2051	0.0052	0.0005	0.0002	0.0204	0.0107
bellii	0.0004	0.0001	0.0065		0.0007	0.0017	0.2232	0.0001	0.302	0.0001	0.0002	0.0001
bibronii	0.0001	0.0001	0.0005	0.0007		0.0156	0.0002	0.0001	0.0002	0.0006	0.0002	0.0212
boulengeri	0.0001	0.0023	0.0255	0.0017	0.0156		0.0024	0.0001	0.0001	0.0001	0.0005	0.0011
buergeri	0.0594	0.0008	0.2051	0.2232	0.0002	0.0024		0.0001	0.0208	0.0002	0.0005	0.0013
canqueli	0.0001	0.6472	0.0052	0.0001	0.0001	0.0001	0.0001		0.0001	0.0182	0.5752	0.1242
ceii	0.0026	0.0001	0.0005	0.302	0.0002	0.0001	0.0208	0.0001		0.0001	0.0001	0.0012
chacabucoense	0.0001	0.0219	0.0002	0.0001	0.0006	0.0001	0.0002	0.0182	0.0001		0.0996	0.9815
chehuachekenk	0.0001	0.6764	0.0204	0.0002	0.0002	0.0005	0.0005	0.5752	0.0001	0.0996		0.318
chiliensis	0.0001	0.1414	0.0107	0.0001	0.0212	0.0011	0.0013	0.1242	0.0012	0.9815	0.318	
coeruleus	0.005	0.0001	0.0005	0.1506	0.0001	0.0001	0.0981	0.0001	0.2207	0.0001	0.0001	0.0002
constanzae	0.0001	0.0001	0.0002	0.0029	0.1247	0.0076	0.0003	0.0001	0.0002	0.0001	0.0001	0.0001
curicensis	0.0001	0.0047	0.0016	0.0001	0.0418	0.0752	0.0002	0.0205	0.0001	0.0049	0.0102	0.0775
curis	0.0842	0.0001	0.0316	0.1069	0.0001	0.0001	0.8137	0.0001	0.0301	0.0001	0.0001	0.0004
darwinni	0.0001	0.0002	0.0037	0.0887	0.461	0.018	0.0088	0.0001	0.0212	0.0004	0.0005	0.0066
elongatus	0.0001	0.0001	0.0001	0.0109	0.0011	0.0001	0.0002	0.0001	0.1373	0.0001	0.0001	0.0002
escarchadosi	0.0001	0.0753	0.0026	0.0001	0.0072	0.0121	0.0001	0.1688	0.0001	0.0267	0.0726	0.1685
fitzingerii	0.0001	0.1177	0.0784	0.0001	0.0001	0.0001	0.0002	0.0015	0.0001	0.0001	0.021	0.0058
gallardoi	0.0704	0.0297	0.6985	0.162	0.0021	0.0334	0.7495	0.0003	0.0082	0.0002	0.0035	0.0026
goetschi	0.0724	0.0653	0.5567	0.4666	0.04	0.1736	0.786	0.0009	0.0165	0.001	0.0056	0.0148
gracilis	0.0001	0.001	0.001	0.0072	0.559	0.0027	0.0012	0.0004	0.0029	0.0086	0.0016	0.1185
grosseorum	0.0001	0.0001	0.0002	0.0001	0.0014	0.0001	0.0002	0.0001	0.0004	0.0096	0.0002	0.1736
irregularis	0.0001	0.0018	0.0078	0.002	0.4198	0.3477	0.0026	0.0006	0.0002	0.0006	0.0018	0.0209
kingii	0.0001	0.0533	0.5796	0.0056	0.0032	0.3021	0.1195	0.0105	0.0006	0.0002	0.0165	0.0182
kolengh	0.0951	0.0001	0.0019	0.0001	0.0001	0.0001	0.0092	0.0001	0.0011	0.0001	0.0001	0.0003
koslowskyi	0.0001	0.0004	0.0008	0.0111	0.6396	0.0031	0.001	0.0001	0.0006	0.0022	0.0005	0.0445

	andinus	archeforus	baguali	bellii	bibronii	boulengeri	buergeri	canqueli	ceii	chacabucoense	chehuachekenk	chiliensis
kriegi	0.133	0.0002	0.1407	0.0012	0.0001	0.0001	0.1339	0.0001	0.0001	0.0001	0.0001	0.0001
lemniscatus	0.0001	0.0001	0.0011	0.0248	0.2164	0.0248	0.0078	0.0001	0.0326	0.0001	0.0001	0.0011
leopardinus	0.0218	0.0003	0.1426	0.2692	0.0003	0.0043	0.9487	0.0001	0.0299	0.0001	0.0002	0.0002
lineomaculatus	0.0001	0.0505	0.273	0.0001	0.0001	0.2087	0.012	0.0134	0.0002	0.0004	0.0115	0.0056
magellanicus	0.0001	0.082	0.0055	0.0001	0.0001	0.0001	0.0002	0.0039	0.0001	0.0015	0.185	0.0756
manueli	0.1011	0.0001	0.0017	0.0603	0.0001	0.0001	0.0859	0.0001	0.1592	0.0001	0.0001	0.0003
melanops	0.0001	0.0478	0.0002	0.0002	0.0005	0.0002	0.0001	0.0813	0.0001	0.1558	0.0633	0.4225
morenoi	0.0001	0.0079	0.0027	0.0007	0.0336	0.0002	0.0018	0.001	0.0077	0.1305	0.0101	0.4671
nigriceps	0.0085	0.0002	0.002	0.0003	0.0001	0.0002	0.0029	0.0002	0.0033	0.0007	0.0007	0.0078
nigroviridis	0.0001	0.0001	0.0002	0.0001	0.3099	0.001	0.0001	0.0003	0.0001	0.0028	0.0002	0.0553
nitidus	0.0001	0.0005	0.0004	0.0001	0.3671	0.055	0.0003	0.0003	0.0001	0.0015	0.0006	0.0284
paulinae	0.0001	0.0001	0.0011	0.0012	0.349	0.0043	0.0025	0.0003	0.0216	0.0045	0.0023	0.068
periglacialis	0.121	0.0001	0.0251	0.0002	0.0001	0.0001	0.0235	0.0001	0.0003	0.0001	0.0001	0.0003
petrophilus	0.0001	0.0001	0.0001	0.0038	0.0032	0.0001	0.0001	0.0001	0.0146	0.0001	0.0001	0.0011
pictus	0.0001	0.0001	0.0001	0.0001	0.0013	0.0001	0.0001	0.0001	0.0025	0.0001	0.0001	0.0001
pseudoanomalus	0.2863	0.0002	0.0153	0.1775	0.0005	0.0005	0.0931	0.001	0.1787	0.0021	0.0022	0.0161
rothi	0.0265	0.0016	0.2684	0.1899	0.0003	0.01	0.9363	0.0001	0.0193	0.0001	0.0002	0.0008
sarmientoi	0.0002	0.176	0.0474	0.0004	0.0003	0.0001	0.0029	0.0079	0.0006	0.005	0.1414	0.1359
scolaroi	0.0001	0.0063	0.0072	0.0001	0.174	0.3149	0.0009	0.0044	0.0001	0.0014	0.0041	0.0407
scroochi	0.6963	0.0151	0.359	0.1364	0.0003	0.0005	0.6074	0.0001	0.0224	0.0005	0.0014	0.0083
shehuen	0.2726	0.8359	0.705	0.6921	0.8387	1	0.4612	0.4985	0.2207	0.2236	0.6196	1
silvanae	0.0103	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
somuncurae	0.0001	0.0375	0.7789	0.0025	0.0005	0.0678	0.0966	0.0032	0.0004	0.0002	0.0102	0.0041
tari	0.0002	0.1623	0.9163	0.0013	0.0002	0.0188	0.084	0.0163	0.0004	0.0004	0.0421	0.0186
telsen	0.0001	0.0001	0.0081	0.1219	0.264	0.0814	0.0267	0.0001	0.0308	0.0003	0.0005	0.0073
tenuis	0.0001	0.0001	0.0001	0.0001	0.5445	0.0008	0.0002	0.0001	0.001	0.0001	0.0001	0.0032
torresi	0.0001	0.0009	0.002	0.0066	0.1984	0.0029	0.0008	0.0009	0.0131	0.003	0.0017	0.0636
tregenzai	0.0346	0.0484	0.7344	0.1623	0.0038	0.0759	0.6541	0.002	0.0031	0.0004	0.0064	0.0154
tristis	0.0002	0.1607	0.6634	0.0004	0.0002	0.0039	0.036	0.0136	0.0004	0.0001	0.0587	0.0192
uptoni	0.0024	0.1006	0.2901	0.1771	0.2229	0.9099	0.1673	0.0037	0.0054	0.004	0.0148	0.0274
wiegmanii	0.0003	0.1573	0.2981	0.0589	0.1627	0.9467	0.0915	0.0474	0.0039	0.0109	0.0525	0.1184
xanthoviridis	0.0001	0.0014	0.001	0.0003	0.4423	0.0569	0.0005	0.0027	0.0006	0.0072	0.0043	0.074
zapallarensis	0.0001	0.0036	0.258	0.0034	0.0027	0.4407	0.0721	0.0014	0.0005	0.0001	0.0021	0.0033
zullyi	0.0001	0.0086	0.007	0.0003	0.4448	0.0758	0.0016	0.0119	0.0009	0.0366	0.0225	0.1978

	coeruleus	constanzae	curicensis	curis	darwinni	elongatus	escarchadosi	fitzingerii	gallardoi	goetschi	gracilis	grosseorum	irregularis
andinus	0.005	0.0001	0.0001	0.0842	0.0001	0.0001	0.0001	0.0001	0.0704	0.0724	0.0001	0.0001	0.0001
archeforus	0.0001	0.0001	0.0047	0.0001	0.0002	0.0001	0.0753	0.1177	0.0297	0.0653	0.001	0.0001	0.0018
baguali	0.0005	0.0002	0.0016	0.0316	0.0037	0.0001	0.0026	0.0784	0.6985	0.5567	0.001	0.0002	0.0078
bellii	0.1506	0.0029	0.0001	0.1069	0.0887	0.0109	0.0001	0.0001	0.162	0.4666	0.0072	0.0001	0.002
bibronii	0.0001	0.1247	0.0418	0.0001	0.461	0.0011	0.0072	0.0001	0.0021	0.04	0.559	0.0014	0.4198
boulengeri	0.0001	0.0076	0.0752	0.0001	0.018	0.0001	0.0121	0.0001	0.0334	0.1736	0.0027	0.0001	0.3477
buergeri	0.0981	0.0003	0.0002	0.8137	0.0088	0.0002	0.0001	0.0002	0.7495	0.786	0.0012	0.0002	0.0026
canqueli	0.0001	0.0001	0.0205	0.0001	0.0001	0.0001	0.1688	0.0015	0.0003	0.0009	0.0004	0.0001	0.0006
ceii	0.2207	0.0002	0.0001	0.0301	0.0212	0.1373	0.0001	0.0001	0.0082	0.0165	0.0029	0.0004	0.0002
chacabucoense	0.0001	0.0001	0.0049	0.0001	0.0004	0.0001	0.0267	0.0001	0.0002	0.001	0.0086	0.0096	0.0006
chehuachekenk	0.0001	0.0001	0.0102	0.0001	0.0005	0.0001	0.0726	0.021	0.0035	0.0056	0.0016	0.0002	0.0018
chiliensis	0.0002	0.0001	0.0775	0.0004	0.0066	0.0002	0.1685	0.0058	0.0026	0.0148	0.1185	0.1736	0.0209
coeruleus		0.0001	0.0001	0.1576	0.0008	0.0003	0.0001	0.0001	0.023	0.0925	0.0002	0.0001	0.0001
constanzae	0.0001		0.0001	0.0001	0.7291	0.0004	0.0001	0.0001	0.0041	0.0696	0.0439	0.0001	0.1855
curicensis	0.0001	0.0001		0.0001	0.0161	0.0001	0.5204	0.0001	0.0034	0.0422	0.0497	0.0002	0.1901
curis	0.1576	0.0001	0.0001		0.0023	0.0003	0.0001	0.0001	0.3933	0.4321	0.001	0.0001	0.0001
darwinni	0.0008	0.7291	0.0161	0.0023		0.0684	0.0012	0.0001	0.0115	0.0885	0.2715	0.0006	0.2966
elongatus	0.0003	0.0004	0.0001	0.0003	0.0684		0.0001	0.0001	0.0018	0.0139	0.0183	0.0002	0.0002
escarchadosi	0.0001	0.0001	0.5204	0.0001	0.0012	0.0001		0.0002	0.0024	0.0124	0.0171	0.0014	0.035
fitzingerii	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0002		0.0065	0.0056	0.0001	0.0001	0.0002
gallardoi	0.023	0.0041	0.0034	0.3933	0.0115	0.0018	0.0024	0.0065		0.8261	0.0009	0.0005	0.0293
goetschi	0.0925	0.0696	0.0422	0.4321	0.0885	0.0139	0.0124	0.0056	0.8261		0.0164	0.0026	0.1779
gracilis	0.0002	0.0439	0.0497	0.001	0.2715	0.0183	0.0171	0.0001	0.0009	0.0164		0.0328	0.1609
grosseorum	0.0001	0.0001	0.0002	0.0001	0.0006	0.0002	0.0014	0.0001	0.0005	0.0026	0.0328		0.0006
irregularis	0.0001	0.1855	0.1901	0.0001	0.2966	0.0002	0.035	0.0002	0.0293	0.1779	0.1609	0.0006	
kingii	0.0001	0.0012	0.0157	0.0065	0.0179	0.0001	0.0195	0.0057	0.5345	0.6621	0.0074	0.0001	0.0643
kolengh	0.0003	0.0001	0.0001	0.0052	0.0001	0.0001	0.0001	0.0001	0.0369	0.0552	0.0002	0.0001	0.0001
koslowskyi	0.0001	0.1067	0.0327	0.0006	0.4246	0.0275	0.0076	0.0001	0.0004	0.0021	0.8409	0.0018	0.1762
kriegi	0.0004	0.0001	0.0001	0.0755	0.0002	0.0001	0.0001	0.0003	0.2087	0.0815	0.0001	0.0001	0.0001
lemniscatus	0.0001	0.8692	0.001	0.0003	0.9165	0.0119	0.0004	0.0001	0.0442	0.2784	0.2133	0.0001	0.2136
leopardinus	0.0711	0.001	0.0001	0.6317	0.0165	0.001	0.0001	0.0002	0.6636	0.8337	0.001	0.0001	0.0047
lineomaculatus	0.0001	0.0001	0.0178	0.0001	0.0027	0.0001	0.0179	0.001	0.1798	0.3158	0.0009	0.0001	0.0264

	coeruleus	constanzae	curicensis	curis	darwinni	elongatus	escarchadosi	fitzingerii	gallardoi	goetschi	gracilis	grosseorum	irregularis
magellanicus	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0007	0.0144	0.0019	0.0019	0.0003	0.0002	0.0003
manueli	0.4833	0.0001	0.0001	0.1585	0.0014	0.0014	0.0001	0.0001	0.0234	0.0591	0.0004	0.0002	0.0001
melanops	0.0001	0.0001	0.1038	0.0001	0.0002	0.0001	0.4178	0.0001	0.0002	0.0004	0.0015	0.0002	0.0027
morenoi	0.0006	0.0003	0.0273	0.0009	0.011	0.001	0.0199	0.0002	0.0053	0.0194	0.0676	0.5453	0.0137
nigriceps	0.0003	0.0001	0.0001	0.0015	0.0017	0.0004	0.0001	0.0001	0.0049	0.0087	0.0083	0.0051	0.0004
nigroviridis	0.0001	0.0002	0.0286	0.0001	0.0594	0.0001	0.0094	0.0001	0.0002	0.0092	0.5942	0.0363	0.0662
nitidus	0.0001	0.0072	0.4148	0.0001	0.0711	0.0001	0.0659	0.0001	0.0012	0.0259	0.1844	0.0003	0.5553
paulinae	0.0001	0.0306	0.0052	0.0002	0.4243	0.0519	0.0033	0.0001	0.0206	0.1014	0.8399	0.0822	0.0802
periglacialis	0.0002	0.0001	0.0001	0.0096	0.0001	0.0001	0.0001	0.0001	0.073	0.0568	0.0001	0.0001	0.0001
petrophilus	0.0001	0.0001	0.0001	0.0001	0.0527	0.7004	0.0001	0.0001	0.0003	0.0025	0.0256	0.0002	0.0006
pictus	0.0001	0.0001	0.0001	0.0001	0.0232	0.2413	0.0001	0.0001	0.0001	0.0009	0.0219	0.0001	0.0002
pseudoanomalus	0.3952	0.0004	0.0002	0.192	0.0048	0.0297	0.0005	0.0001	0.0232	0.0344	0.0179	0.0139	0.0007
rothi	0.0399	0.0015	0.0001	0.5519	0.0136	0.0009	0.0001	0.0005	0.8234	0.8832	0.0005	0.0001	0.0069
sarmientoi	0.0001	0.0001	0.0007	0.0005	0.0011	0.0003	0.0031	0.1127	0.0123	0.0254	0.0077	0.0016	0.0006
scolaroi	0.0001	0.01	0.7014	0.0001	0.0636	0.0001	0.1991	0.0001	0.0099	0.0846	0.0836	0.0002	0.6476
scroochi	0.0953	0.0003	0.0003	0.5747	0.0028	0.0028	0.0001	0.0034	0.4259	0.1574	0.0087	0.0022	0.0028
shehuen	0.3443	0.744	0.8861	0.3387	1	0.4325	0.7024	0.2007	0.6626	0.6652	0.66	0.1402	0.9541
silvanae	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0004	0.0005	0.0001	0.0001	0.0001
somuncurae	0.0002	0.0001	0.0024	0.008	0.0036	0.0002	0.0021	0.0083	0.5159	0.5093	0.0004	0.0001	0.0118
tari	0.0001	0.0001	0.0027	0.0076	0.0025	0.0001	0.0061	0.1861	0.4858	0.4249	0.0006	0.0001	0.0058
telsen	0.0009	0.9342	0.014	0.0017	0.7789	0.0201	0.001	0.0001	0.0601	0.2883	0.1502	0.0005	0.3793
tenuis	0.0001	0.0714	0.0009	0.0001	0.6648	0.0033	0.0002	0.0001	0.0013	0.0279	0.5873	0.0008	0.0832
torresi	0.0005	0.0232	0.0045	0.0017	0.2687	0.1025	0.0036	0.0002	0.0081	0.0493	0.6494	0.0405	0.0504
tregenzai	0.0171	0.005	0.0074	0.3167	0.0139	0.0013	0.002	0.0069	0.9741	0.8571	0.0052	0.0009	0.0501
tristis	0.0001	0.0001	0.0004	0.0033	0.0019	0.0001	0.003	0.5399	0.2654	0.2242	0.0014	0.0001	0.0021
uptoni	0.0039	0.2646	0.2928	0.054	0.2334	0.0105	0.1079	0.003	0.2258	0.3705	0.025	0.0022	0.6763
wiegmanii	0.0012	0.0911	0.4463	0.0124	0.141	0.0035	0.2409	0.0043	0.2399	0.3956	0.0709	0.0016	0.6045
xanthoviridis	0.0001	0.0095	0.3647	0.0001	0.1372	0.0003	0.0966	0.0001	0.007	0.0686	0.3092	0.0103	0.4807
zapallarensis	0.0001	0.0011	0.0062	0.0023	0.0213	0.0001	0.0047	0.0002	0.4189	0.6906	0.0048	0.0001	0.0704
zullyi	0.0001	0.02	0.5474	0.0001	0.1634	0.0005	0.236	0.0001	0.0174	0.0852	0.4185	0.0383	0.4393

	kingii	kolengh	koslowskyi	kriegi	lemniscatus	leopardinus	lineomaculatus	magellanicus	manueli	melanops	morenoi	nigriceps	nigroviridis
andinus	0.0001	0.0951	0.0001	0.133	0.0001	0.0218	0.0001	0.0001	0.1011	0.0001	0.0001	0.0085	0.0001
archeforus	0.0533	0.0001	0.0004	0.0002	0.0001	0.0003	0.0505	0.082	0.0001	0.0478	0.0079	0.0002	0.0001
baguali	0.5796	0.0019	0.0008	0.1407	0.0011	0.1426	0.273	0.0055	0.0017	0.0002	0.0027	0.002	0.0002
bellii	0.0056	0.0001	0.0111	0.0012	0.0248	0.2692	0.0001	0.0001	0.0603	0.0002	0.0007	0.0003	0.0001
bibronii	0.0032	0.0001	0.6396	0.0001	0.2164	0.0003	0.0001	0.0001	0.0001	0.0005	0.0336	0.0001	0.3099
boulengeri	0.3021	0.0001	0.0031	0.0001	0.0248	0.0043	0.2087	0.0001	0.0001	0.0002	0.0002	0.0002	0.001
buergeri	0.1195	0.0092	0.001	0.1339	0.0078	0.9487	0.012	0.0002	0.0859	0.0001	0.0018	0.0029	0.0001
canqueli	0.0105	0.0001	0.0001	0.0001	0.0001	0.0001	0.0134	0.0039	0.0001	0.0813	0.001	0.0002	0.0003
ceii	0.0006	0.0011	0.0006	0.0001	0.0326	0.0299	0.0002	0.0001	0.1592	0.0001	0.0077	0.0033	0.0001
chacabucoense	0.0002	0.0001	0.0022	0.0001	0.0001	0.0001	0.0004	0.0015	0.0001	0.1558	0.1305	0.0007	0.0028
chehuachekenk	0.0165	0.0001	0.0005	0.0001	0.0001	0.0002	0.0115	0.185	0.0001	0.0633	0.0101	0.0007	0.0002
chiliensis	0.0182	0.0003	0.0445	0.0001	0.0011	0.0002	0.0056	0.0756	0.0003	0.4225	0.4671	0.0078	0.0553
Coeruleus	0.0001	0.0003	0.0001	0.0004	0.0001	0.0711	0.0001	0.0001	0.4833	0.0001	0.0006	0.0003	0.0001
constanzae	0.0012	0.0001	0.1067	0.0001	0.8692	0.001	0.0001	0.0001	0.0001	0.0001	0.0003	0.0001	0.0002
curicensis	0.0157	0.0001	0.0327	0.0001	0.001	0.0001	0.0178	0.0001	0.0001	0.1038	0.0273	0.0001	0.0286
curis	0.0065	0.0052	0.0006	0.0755	0.0003	0.6317	0.0001	0.0001	0.1585	0.0001	0.0009	0.0015	0.0001
darwinni	0.0179	0.0001	0.4246	0.0002	0.9165	0.0165	0.0027	0.0001	0.0014	0.0002	0.011	0.0017	0.0594
elongatus	0.0001	0.0001	0.0275	0.0001	0.0119	0.001	0.0001	0.0001	0.0014	0.0001	0.001	0.0004	0.0001
escarchadosi	0.0195	0.0001	0.0076	0.0001	0.0004	0.0001	0.0179	0.0007	0.0001	0.4178	0.0199	0.0001	0.0094
fitzingerii	0.0057	0.0001	0.0001	0.0003	0.0001	0.0002	0.001	0.0144	0.0001	0.0001	0.0002	0.0001	0.0001
gallardoi	0.5345	0.0369	0.0004	0.2087	0.0442	0.6636	0.1798	0.0019	0.0234	0.0002	0.0053	0.0049	0.0002
goetschi	0.6621	0.0552	0.0021	0.0815	0.2784	0.8337	0.3158	0.0019	0.0591	0.0004	0.0194	0.0087	0.0092
gracilis	0.0074	0.0002	0.8409	0.0001	0.2133	0.001	0.0009	0.0003	0.0004	0.0015	0.0676	0.0083	0.5942
Grosseorum	0.0001	0.0001	0.0018	0.0001	0.0001	0.0001	0.0001	0.0002	0.0002	0.0002	0.5453	0.0051	0.0363
irregularis	0.0643	0.0001	0.1762	0.0001	0.2136	0.0047	0.0264	0.0003	0.0001	0.0027	0.0137	0.0004	0.0662
kingii		0.0001	0.006	0.0102	0.0043	0.1089	0.8161	0.0003	0.0001	0.001	0.0024	0.0006	0.0002
kolengh	0.0001		0.0001	0.0958	0.0001	0.0036	0.0001	0.0001	0.0179	0.0001	0.0001	0.2619	0.0001
koslowskyi	0.006	0.0001		0.0001	0.3506	0.0024	0.0007	0.0001	0.0002	0.0005	0.0235	0.0047	0.3907
kriegi	0.0102	0.0958	0.0001		0.0001	0.0623	0.0002	0.0001	0.0029	0.0001	0.0011	0.0057	0.0001
lemniscatus	0.0043	0.0001	0.3506	0.0001		0.0108	0.0007	0.0001	0.0002	0.0001	0.0072	0.0001	0.0008
leopardinus	0.1089	0.0036	0.0024	0.0623	0.0108		0.0066	0.0001	0.0478	0.0001	0.001	0.0028	0.0001
lineomaculatus	0.8161	0.0001	0.0007	0.0002	0.0007	0.0066		0.0003	0.0001	0.0013	0.0001	0.0001	0.0001

	kingii	kolengh	koslowskyi	kriegi	lemniscatus	leopardinus	lineomaculatus	magellanicus	manueli	melanops	morenoi	nigriceps	nigroviridis
magellanicus	0.0003	0.0001	0.0001	0.0001	0.0001	0.0001	0.0003		0.0001	0.0003	0.0041	0.0045	0.0001
manueli	0.0001	0.0179	0.0002	0.0029	0.0002	0.0478	0.0001	0.0001		0.0001	0.0025	0.0053	0.0001
melanops	0.001	0.0001	0.0005	0.0001	0.0001	0.0001	0.0013	0.0003	0.0001		0.0038	0.0002	0.0086
morenoi	0.0024	0.0001	0.0235	0.0011	0.0072	0.001	0.0001	0.0041	0.0025	0.0038		0.029	0.162
nigriceps	0.0006	0.2619	0.0047	0.0057	0.0001	0.0028	0.0001	0.0045	0.0053	0.0002	0.029		0.0001
nigroviridis	0.0002	0.0001	0.3907	0.0001	0.0008	0.0001	0.0001	0.0001	0.0001	0.0086	0.162	0.0001	
nitidus	0.0081	0.0001	0.1308	0.0001	0.0238	0.0001	0.0041	0.0001	0.0001	0.0058	0.0246	0.0001	0.2794
paulinae	0.002	0.0001	0.9024	0.0002	0.0771	0.0027	0.0007	0.0003	0.0002	0.0042	0.185	0.0012	0.089
periglacialis	0.0003	0.4518	0.0002	0.4357	0.0001	0.0066	0.0001	0.0002	0.0048	0.0001	0.0005	0.0724	0.0001
petrophilus	0.0001	0.0001	0.0302	0.0001	0.0174	0.0005	0.0001	0.0001	0.0001	0.0001	0.0045	0.0009	0.0002
pictus	0.0001	0.0001	0.0301	0.0001	0.0011	0.0001	0.0001	0.0001	0.0001	0.0001	0.0012	0.0002	0.0001
pseudoanomalus	0.0049	0.2068	0.0131	0.0104	0.018	0.076	0.0007	0.0021	0.8285	0.0013	0.1042	0.0578	0.0001
rothi	0.2125	0.0074	0.0014	0.1018	0.015	0.932	0.0251	0.0002	0.032	0.0001	0.0017	0.003	0.0001
sarmientoi	0.0111	0.009	0.003	0.002	0.0001	0.0019	0.0029	0.7974	0.0008	0.0007	0.0355	0.0634	0.0001
scolaroi	0.0722	0.0001	0.0545	0.0001	0.03	0.0003	0.0552	0.0001	0.0001	0.0185	0.0069	0.0003	0.0758
scroochi	0.1454	0.4079	0.0026	0.7974	0.0188	0.4118	0.0194	0.0032	0.2079	0.0001	0.0163	0.0392	0.0001
shehuen	0.824	0.216	0.5686	0.222	0.8846	0.5588	0.815	0.2322	0.3812	0.3903	0.2508	0.2004	0.8081
silvanae	0.0001	0.9414	0.0001	0.0064	0.0001	0.0001	0.0001	0.0001	0.0004	0.0001	0.0002	0.0808	0.0001
somuncurae	0.8711	0.0001	0.0005	0.0132	0.0017	0.0794	0.5196	0.0009	0.0001	0.0003	0.0001	0.0003	0.0001
tari	0.5418	0.0008	0.0009	0.0554	0.0006	0.0579	0.3342	0.0088	0.0005	0.0001	0.0033	0.0033	0.0001
telsen	0.0436	0.0001	0.2235	0.0001	0.9433	0.0372	0.0075	0.0001	0.0018	0.0003	0.0119	0.0004	0.0112
tenuis	0.0003	0.0001	0.8577	0.0001	0.1685	0.0001	0.0001	0.0001	0.0001	0.0002	0.0133	0.0001	0.0221
torresi	0.0033	0.0001	0.5501	0.0004	0.1374	0.0023	0.0003	0.0009	0.0014	0.0017	0.1133	0.0169	0.0987
tregenzai	0.6708	0.0214	0.0018	0.1405	0.058	0.6457	0.2856	0.0016	0.0214	0.0003	0.0055	0.0062	0.0009
tristis	0.1934	0.0011	0.0006	0.0691	0.0002	0.0236	0.0775	0.0255	0.0001	0.0006	0.0008	0.0077	0.0001
uptoni	0.6972	0.0036	0.0412	0.0035	0.4578	0.2035	0.504	0.0011	0.0037	0.0031	0.0114	0.0043	0.1006
wiegmanii	0.7248	0.001	0.0479	0.0016	0.2003	0.1005	0.7086	0.0025	0.0022	0.031	0.0304	0.002	0.0735
xanthoviridis	0.0087	0.0001	0.2547	0.0001	0.0283	0.0003	0.0052	0.0001	0.0001	0.0347	0.086	0.0001	0.4435
zapallarensis	0.8333	0.0001	0.0066	0.0016	0.0042	0.0823	0.4869	0.0003	0.0001	0.0006	0.001	0.0001	0.0001
zullyi	0.0294	0.0001	0.3033	0.0001	0.0522	0.0009	0.0162	0.0003	0.0001	0.1109	0.1914	0.0009	0.6588

	nitidus	paulinae	periglacialis	petrophilus	pictus	pseudoanomalus	rothi	sarmientoi	scolaroi	scroochi	shehuen	silvanae
andinus	0.0001	0.0001	0.121	0.0001	0.0001	0.2863	0.0265	0.0002	0.0001	0.6963	0.2726	0.0103
archeforus	0.0005	0.0001	0.0001	0.0001	0.0001	0.0002	0.0016	0.176	0.0063	0.0151	0.8359	0.0001
baguali	0.0004	0.0011	0.0251	0.0001	0.0001	0.0153	0.2684	0.0474	0.0072	0.359	0.705	0.0001
bellii	0.0001	0.0012	0.0002	0.0038	0.0001	0.1775	0.1899	0.0004	0.0001	0.1364	0.6921	0.0001
bibronii	0.3671	0.349	0.0001	0.0032	0.0013	0.0005	0.0003	0.0003	0.174	0.0003	0.8387	0.0001
boulengeri	0.055	0.0043	0.0001	0.0001	0.0001	0.0005	0.01	0.0001	0.3149	0.0005	1	0.0001
buergeri	0.0003	0.0025	0.0235	0.0001	0.0001	0.0931	0.9363	0.0029	0.0009	0.6074	0.4612	0.0001
canqueli	0.0003	0.0003	0.0001	0.0001	0.0001	0.001	0.0001	0.0079	0.0044	0.0001	0.4985	0.0001
ceii	0.0001	0.0216	0.0003	0.0146	0.0025	0.1787	0.0193	0.0006	0.0001	0.0224	0.2207	0.0001
chacabucoense	0.0015	0.0045	0.0001	0.0001	0.0001	0.0021	0.0001	0.005	0.0014	0.0005	0.2236	0.0001
chehuachekenk	0.0006	0.0023	0.0001	0.0001	0.0001	0.0022	0.0002	0.1414	0.0041	0.0014	0.6196	0.0001
chiliensis	0.0284	0.068	0.0003	0.0011	0.0001	0.0161	0.0008	0.1359	0.0407	0.0083	1	0.0001
coeruleus	0.0001	0.0001	0.0002	0.0001	0.0001	0.3952	0.0399	0.0001	0.0001	0.0953	0.3443	0.0001
constanzae	0.0072	0.0306	0.0001	0.0001	0.0001	0.0004	0.0015	0.0001	0.01	0.0003	0.744	0.0001
curicensis	0.4148	0.0052	0.0001	0.0001	0.0001	0.0002	0.0001	0.0007	0.7014	0.0003	0.8861	0.0001
curis	0.0001	0.0002	0.0096	0.0001	0.0001	0.192	0.5519	0.0005	0.0001	0.5747	0.3387	0.0001
darwinni	0.0711	0.4243	0.0001	0.0527	0.0232	0.0048	0.0136	0.0011	0.0636	0.0028	1	0.0001
elongatus	0.0001	0.0519	0.0001	0.7004	0.2413	0.0297	0.0009	0.0003	0.0001	0.0028	0.4325	0.0001
escarchadosi	0.0659	0.0033	0.0001	0.0001	0.0001	0.0005	0.0001	0.0031	0.1991	0.0001	0.7024	0.0001
fitzingerii	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0005	0.1127	0.0001	0.0034	0.2007	0.0001
gallardoi	0.0012	0.0206	0.073	0.0003	0.0001	0.0232	0.8234	0.0123	0.0099	0.4259	0.6626	0.0004
goetschi	0.0259	0.1014	0.0568	0.0025	0.0009	0.0344	0.8832	0.0254	0.0846	0.1574	0.6652	0.0005
gracilis	0.1844	0.8399	0.0001	0.0256	0.0219	0.0179	0.0005	0.0077	0.0836	0.0087	0.66	0.0001
grosseorum	0.0003	0.0822	0.0001	0.0002	0.0001	0.0139	0.0001	0.0016	0.0002	0.0022	0.1402	0.0001
irregularis	0.5553	0.0802	0.0001	0.0006	0.0002	0.0007	0.0069	0.0006	0.6476	0.0028	0.9541	0.0001
kingii	0.0081	0.002	0.0003	0.0001	0.0001	0.0049	0.2125	0.0111	0.0722	0.1454	0.824	0.0001
kolengh	0.0001	0.0001	0.4518	0.0001	0.0001	0.2068	0.0074	0.009	0.0001	0.4079	0.216	0.9414
koslowskyi	0.1308	0.9024	0.0002	0.0302	0.0301	0.0131	0.0014	0.003	0.0545	0.0026	0.5686	0.0001
kriegi	0.0001	0.0002	0.4357	0.0001	0.0001	0.0104	0.1018	0.002	0.0001	0.7974	0.222	0.0064
lemniscatus	0.0238	0.0771	0.0001	0.0174	0.0011	0.018	0.015	0.0001	0.03	0.0188	0.8846	0.0001
leopardinus	0.0001	0.0027	0.0066	0.0005	0.0001	0.076	0.932	0.0019	0.0003	0.4118	0.5588	0.0001
lineomaculatus	0.0041	0.0007	0.0001	0.0001	0.0001	0.0007	0.0251	0.0029	0.0552	0.0194	0.815	0.0001

	nitidus	paulinae	periglacialis	petrophilus	pictus	pseudoanomalus	rothi	sarmientoi	scolaroi	scroochi	shehuen	silvanae
magellanicus	0.0001	0.0003	0.0002	0.0001	0.0001	0.0021	0.0002	0.7974	0.0001	0.0032	0.2322	0.0001
manueli	0.0001	0.0002	0.0048	0.0001	0.0001	0.8285	0.032	0.0008	0.0001	0.2079	0.3812	0.0004
melanops	0.0058	0.0042	0.0001	0.0001	0.0001	0.0013	0.0001	0.0007	0.0185	0.0001	0.3903	0.0001
morenoi	0.0246	0.185	0.0005	0.0045	0.0012	0.1042	0.0017	0.0355	0.0069	0.0163	0.2508	0.0002
nigriceps	0.0001	0.0012	0.0724	0.0009	0.0002	0.0578	0.003	0.0634	0.0003	0.0392	0.2004	0.0808
nigroviridis	0.2794	0.089	0.0001	0.0002	0.0001	0.0001	0.0001	0.0001	0.0758	0.0001	0.8081	0.0001
nitidus		0.0571	0.0001	0.0001	0.0001	0.0005	0.0001	0.0002	0.7076	0.0005	0.8835	0.0001
paulinae	0.0571		0.0001	0.154	0.0948	0.0374	0.0033	0.0063	0.0368	0.0196	0.5613	0.0001
periglacialis	0.0001	0.0001		0.0001	0.0001	0.0596	0.0135	0.0125	0.0001	0.5754	0.2753	0.2751
petrophilus	0.0001	0.154	0.0001		0.7358	0.0041	0.0004	0.0005	0.0001	0.0011	0.1809	0.0001
pictus	0.0001	0.0948	0.0001	0.7358		0.0012	0.0002	0.0001	0.0001	0.0001	0.1632	0.0001
pseudoanomalus	0.0005	0.0374	0.0596	0.0041	0.0012		0.0731	0.0361	0.0006	0.0381	0.2543	0.0228
rothi	0.0001	0.0033	0.0135	0.0004	0.0002	0.0731		0.0028	0.0011	0.4242	0.6729	0.0001
sarmientoi	0.0002	0.0063	0.0125	0.0005	0.0001	0.0361	0.0028		0.0002	0.0336	0.3424	0.0005
scolaroi	0.7076	0.0368	0.0001	0.0001	0.0001	0.0006	0.0011	0.0002		0.0008	1	0.0001
scroochi	0.0005	0.0196	0.5754	0.0011	0.0001	0.0381	0.4242	0.0336	0.0008		0.3353	0.1217
shehuen	0.8835	0.5613	0.2753	0.1809	0.1632	0.2543	0.6729	0.3424	1	0.3353		0.0522
silvanae	0.0001	0.0001	0.2751	0.0001	0.0001	0.0228	0.0001	0.0005	0.0001	0.1217	0.0522	
somuncurae	0.0005	0.0005	0.0005	0.0001	0.0001	0.0042	0.1677	0.0125	0.0107	0.1263	0.7917	0.0001
tari	0.0002	0.001	0.0096	0.0001	0.0001	0.01	0.1239	0.0745	0.0065	0.2233	0.7834	0.0001
telsen	0.0626	0.1464	0.0001	0.0193	0.0031	0.0102	0.0414	0.0009	0.087	0.0162	0.9341	0.0001
tenuis	0.0309	0.5263	0.0001	0.0149	0.0036	0.0004	0.0003	0.0002	0.0134	0.0005	0.8249	0.0001
torresi	0.0225	0.8509	0.0002	0.1862	0.2232	0.0352	0.0046	0.0162	0.0149	0.033	0.4952	0.0001
tregenzai	0.0046	0.0223	0.0395	0.0004	0.0001	0.0478	0.8123	0.0065	0.0263	0.3059	0.446	0.0001
tristis	0.0004	0.0003	0.0182	0.0001	0.0001	0.003	0.0587	0.1706	0.0028	0.1974	0.7293	0.0001
uptoni	0.286	0.1686	0.0012	0.0043	0.0012	0.0113	0.212	0.008	0.5304	0.0042	1	0.0001
wiegmanii	0.3188	0.103	0.0006	0.0018	0.0003	0.018	0.1279	0.019	0.6707	0.0464	1	0.0001
xanthoviridis	0.9604	0.0902	0.0001	0.0007	0.0001	0.0012	0.0003	0.0007	0.5719	0.0024	0.8808	0.0001
zapallarensis	0.0035	0.0012	0.0001	0.0001	0.0001	0.0044	0.1539	0.0028	0.0582	0.0718	0.9443	0.0001
zullyi	0.8807	0.1647	0.0001	0.0019	0.0002	0.0061	0.002	0.0071	0.6119	0.0054	0.9338	0.0001

	somuncurae	tari	telsen	tenuis	torresi	tregenzai	tristis	uptoni	wiegmanii	xanthoviridis	zapallarensis	zullyi
andinus	0.0001	0.0002	0.0001	0.0001	0.0001	0.0346	0.0002	0.0024	0.0003	0.0001	0.0001	0.0001
archeforus	0.0375	0.1623	0.0001	0.0001	0.0009	0.0484	0.1607	0.1006	0.1573	0.0014	0.0036	0.0086
baguali	0.7789	0.9163	0.0081	0.0001	0.002	0.7344	0.6634	0.2901	0.2981	0.001	0.258	0.007
bellii	0.0025	0.0013	0.1219	0.0001	0.0066	0.1623	0.0004	0.1771	0.0589	0.0003	0.0034	0.0003
bibronii	0.0005	0.0002	0.264	0.5445	0.1984	0.0038	0.0002	0.2229	0.1627	0.4423	0.0027	0.4448
boulengeri	0.0678	0.0188	0.0814	0.0008	0.0029	0.0759	0.0039	0.9099	0.9467	0.0569	0.4407	0.0758
buergeri	0.0966	0.084	0.0267	0.0002	0.0008	0.6541	0.036	0.1673	0.0915	0.0005	0.0721	0.0016
canqueli	0.0032	0.0163	0.0001	0.0001	0.0009	0.002	0.0136	0.0037	0.0474	0.0027	0.0014	0.0119
ceii	0.0004	0.0004	0.0308	0.001	0.0131	0.0031	0.0004	0.0054	0.0039	0.0006	0.0005	0.0009
chacabucoense	0.0002	0.0004	0.0003	0.0001	0.003	0.0004	0.0001	0.004	0.0109	0.0072	0.0001	0.0366
chehuachekenk	0.0102	0.0421	0.0005	0.0001	0.0017	0.0064	0.0587	0.0148	0.0525	0.0043	0.0021	0.0225
chiliensis	0.0041	0.0186	0.0073	0.0032	0.0636	0.0154	0.0192	0.0274	0.1184	0.074	0.0033	0.1978
coeruleus	0.0002	0.0001	0.0009	0.0001	0.0005	0.0171	0.0001	0.0039	0.0012	0.0001	0.0001	0.0001
constanzae	0.0001	0.0001	0.9342	0.0714	0.0232	0.005	0.0001	0.2646	0.0911	0.0095	0.0011	0.02
curicensis	0.0024	0.0027	0.014	0.0009	0.0045	0.0074	0.0004	0.2928	0.4463	0.3647	0.0062	0.5474
curis	0.008	0.0076	0.0017	0.0001	0.0017	0.3167	0.0033	0.054	0.0124	0.0001	0.0023	0.0001
darwinni	0.0036	0.0025	0.7789	0.6648	0.2687	0.0139	0.0019	0.2334	0.141	0.1372	0.0213	0.1634
elongatus	0.0002	0.0001	0.0201	0.0033	0.1025	0.0013	0.0001	0.0105	0.0035	0.0003	0.0001	0.0005
escarchadosi	0.0021	0.0061	0.001	0.0002	0.0036	0.002	0.003	0.1079	0.2409	0.0966	0.0047	0.236
fitzingerii	0.0083	0.1861	0.0001	0.0001	0.0002	0.0069	0.5399	0.003	0.0043	0.0001	0.0002	0.0001
gallardoi	0.5159	0.4858	0.0601	0.0013	0.0081	0.9741	0.2654	0.2258	0.2399	0.007	0.4189	0.0174
goetschi	0.5093	0.4249	0.2883	0.0279	0.0493	0.8571	0.2242	0.3705	0.3956	0.0686	0.6906	0.0852
gracilis	0.0004	0.0006	0.1502	0.5873	0.6494	0.0052	0.0014	0.025	0.0709	0.3092	0.0048	0.4185
grosseorum	0.0001	0.0001	0.0005	0.0008	0.0405	0.0009	0.0001	0.0022	0.0016	0.0103	0.0001	0.0383
irregularis	0.0118	0.0058	0.3793	0.0832	0.0504	0.0501	0.0021	0.6763	0.6045	0.4807	0.0704	0.4393
kingii	0.8711	0.5418	0.0436	0.0003	0.0033	0.6708	0.1934	0.6972	0.7248	0.0087	0.8333	0.0294
kolengh	0.0001	0.0008	0.0001	0.0001	0.0001	0.0214	0.0011	0.0036	0.001	0.0001	0.0001	0.0001
koslowskyi	0.0005	0.0009	0.2235	0.8577	0.5501	0.0018	0.0006	0.0412	0.0479	0.2547	0.0066	0.3033
kriegi	0.0132	0.0554	0.0001	0.0001	0.0004	0.1405	0.0691	0.0035	0.0016	0.0001	0.0016	0.0001
lemniscatus	0.0017	0.0006	0.9433	0.1685	0.1374	0.058	0.0002	0.4578	0.2003	0.0283	0.0042	0.0522
leopardinus	0.0794	0.0579	0.0372	0.0001	0.0023	0.6457	0.0236	0.2035	0.1005	0.0003	0.0823	0.0009
lineomaculatus	0.5196	0.3342	0.0075	0.0001	0.0003	0.2856	0.0775	0.504	0.7086	0.0052	0.4869	0.0162

	somuncurae	tari	telsen	tenuis	torresi	tregenzai	tristis	uptoni	wiegmanii	xanthoviridis	zapallarensis	zullyi
magellanicus	0.0009	0.0088	0.0001	0.0001	0.0009	0.0016	0.0255	0.0011	0.0025	0.0001	0.0003	0.0003
manueli	0.0001	0.0005	0.0018	0.0001	0.0014	0.0214	0.0001	0.0037	0.0022	0.0001	0.0001	0.0001
melanops	0.0003	0.0001	0.0003	0.0002	0.0017	0.0003	0.0006	0.0031	0.031	0.0347	0.0006	0.1109
morenoi	0.0001	0.0033	0.0119	0.0133	0.1133	0.0055	0.0008	0.0114	0.0304	0.086	0.001	0.1914
nigriceps	0.0003	0.0033	0.0004	0.0001	0.0169	0.0062	0.0077	0.0043	0.002	0.0001	0.0001	0.0009
nigroviridis	0.0001	0.0001	0.0112	0.0221	0.0987	0.0009	0.0001	0.1006	0.0735	0.4435	0.0001	0.6588
nitidus	0.0005	0.0002	0.0626	0.0309	0.0225	0.0046	0.0004	0.286	0.3188	0.9604	0.0035	0.8807
paulinae	0.0005	0.001	0.1464	0.5263	0.8509	0.0223	0.0003	0.1686	0.103	0.0902	0.0012	0.1647
periglacialis	0.0005	0.0096	0.0001	0.0001	0.0002	0.0395	0.0182	0.0012	0.0006	0.0001	0.0001	0.0001
petrophilus	0.0001	0.0001	0.0193	0.0149	0.1862	0.0004	0.0001	0.0043	0.0018	0.0007	0.0001	0.0019
pictus	0.0001	0.0001	0.0031	0.0036	0.2232	0.0001	0.0001	0.0012	0.0003	0.0001	0.0001	0.0002
pseudoanomalus	0.0042	0.01	0.0102	0.0004	0.0352	0.0478	0.003	0.0113	0.018	0.0012	0.0044	0.0061
rothi	0.1677	0.1239	0.0414	0.0003	0.0046	0.8123	0.0587	0.212	0.1279	0.0003	0.1539	0.002
sarmientoi	0.0125	0.0745	0.0009	0.0002	0.0162	0.0065	0.1706	0.008	0.019	0.0007	0.0028	0.0071
scolaroi	0.0107	0.0065	0.087	0.0134	0.0149	0.0263	0.0028	0.5304	0.6707	0.5719	0.0582	0.6119
scroochi	0.1263	0.2233	0.0162	0.0005	0.033	0.3059	0.1974	0.0042	0.0464	0.0024	0.0718	0.0054
shehuen	0.7917	0.7834	0.9341	0.8249	0.4952	0.446	0.7293	1	1	0.8808	0.9443	0.9338
silvanae	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
somuncurae		0.7207	0.0116	0.0001	0.0006	0.6615	0.2918	0.3478	0.3946	0.0016	0.4811	0.0055
tari	0.7207		0.005	0.0001	0.0019	0.536	0.7967	0.2457	0.3067	0.0012	0.1876	0.0063
telsen	0.0116	0.005		0.2168	0.0984	0.0884	0.0008	0.4974	0.277	0.0897	0.0515	0.1163
tenuis	0.0001	0.0001	0.2168		0.3762	0.002	0.0001	0.115	0.0456	0.0575	0.0001	0.0869
torresi	0.0006	0.0019	0.0984	0.3762		0.0134	0.0016	0.0824	0.0431	0.0676	0.0026	0.1199
tregenzai	0.6615	0.536	0.0884	0.002	0.0134		0.291	0.3566	0.337	0.0135	0.5748	0.022
tristis	0.2918	0.7967	0.0008	0.0001	0.0016	0.291		0.1059	0.1326	0.0001	0.0356	0.0022
uptoni	0.3478	0.2457	0.4974	0.115	0.0824	0.3566	0.1059		0.9014	0.2872	0.8244	0.3273
wiegmanii	0.3946	0.3067	0.277	0.0456	0.0431	0.337	0.1326	0.9014		0.2984	0.7485	0.3824
xanthoviridis	0.0016	0.0012	0.0897	0.0575	0.0676	0.0135	0.0001	0.2872	0.2984		0.0059	0.9314
zapallarensis	0.4811	0.1876	0.0515	0.0001	0.0026	0.5748	0.0356	0.8244	0.7485	0.0059		0.0155
zullyi	0.0055	0.0063	0.1163	0.0869	0.1199	0.022	0.0022	0.3273	0.3824	0.9314	0.0155	